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Genetic potential of Portuguese maize germplasm with abnormal ear shape

by

Silas Esteves Pego

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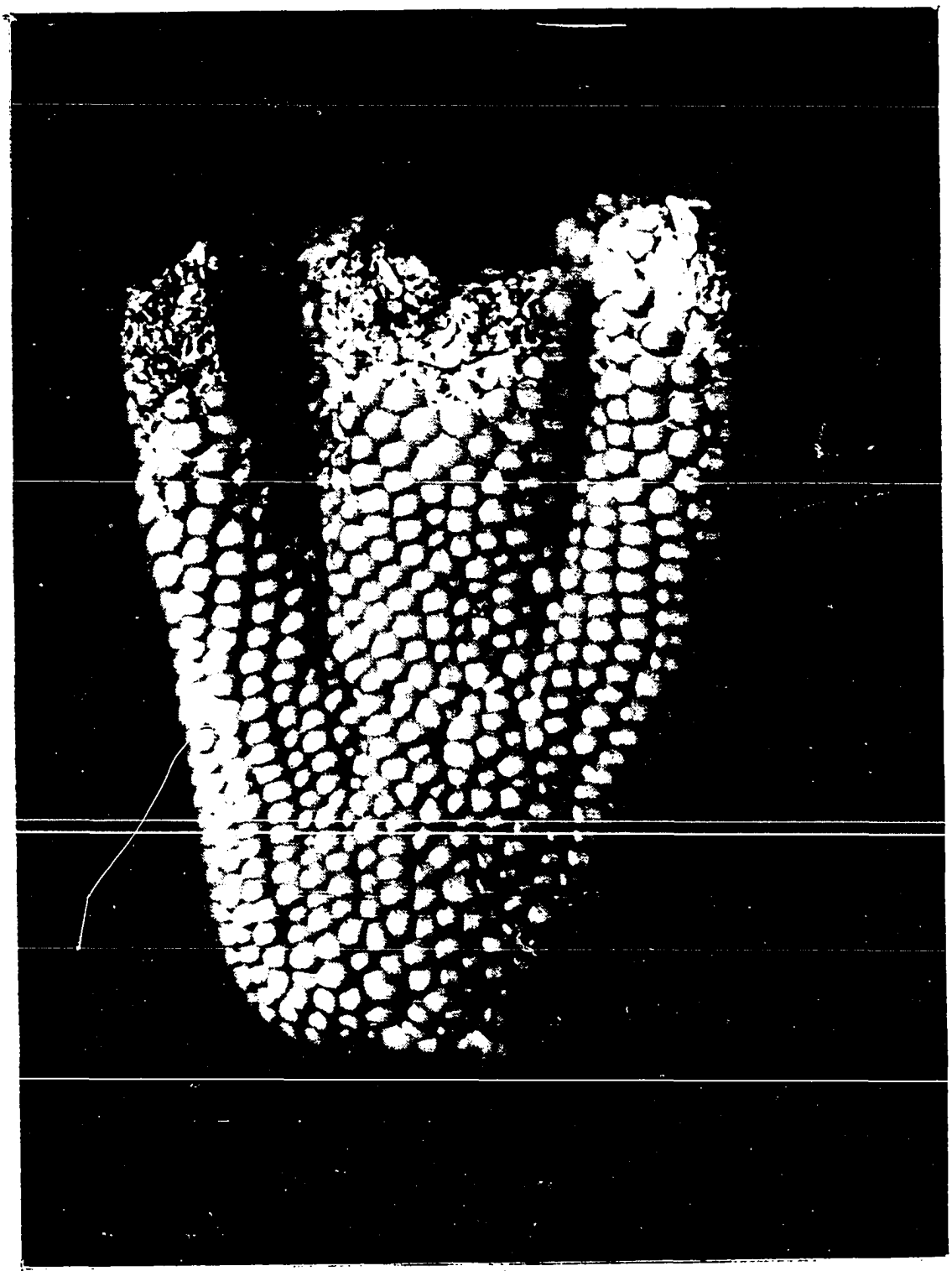
RELIC RACES...

Although obvious fasciation is rare in modern maize, it does occur in extreme form in certain relic races....

Galinat (1963)



I. INTRODUCTION

The author was assigned to an advanced maize (Zea mays L.) breeding program of introducing fasciated germplasm into some original U.S. inbreds at a governmental maize breeding station in northern Portugal (Braga). The program was oriented to increasing the kernel-row number in some inbreds using the backcross breeding procedure. As a result of that breeding program, a double-cross hybrid (HB19) had been developed and was being used by some farmers in the northern part of Portugal. HB19 was, however, still in a process of refinement because of its high ear placement and lack of uniformity in the shape of the ears which constituted a barrier to the farmer's acceptance. Nevertheless, HB19 was performing reasonably well for yield, and two of its characteristics were a kernel-row number that averaged 20 rows per ear and a kernel depth of about 14 mm.

Interest in this type of germplasm was increased in 1976 when the author was directing a germplasm collection of maize with the collaboration of the official Portuguese Extension Service. During the process of collection, some samples were observed that had not only a very high percentage (above 90%) of abnormal ears, but also a very intense expression of the character. Such an abnormal ear shape seemed to suggest intermediate expression between the fasciation and ramosa 1 (ra1) phenotypic expressions. The author's

interest was directed to the fact that those open-pollinated varieties, preferred by a few farmers, were grown in small areas that were surrounded by other nonfasciated open-pollinated varieties. Although the fasciated varieties were surrounded by varieties that had normal ears, they maintained a high level of fasciation expression. A hypothesis of dominance was suggested for the expression of the abnormal ears. Because some plants displayed an intense tassel branching, the hypothesis of allelism with ramosa 1 (ral) gene also was considered. Because the fasciated germplasm was characterized by a high kernel-row number, the immediate practical value of the germplasm was to use it as a good source for increasing kernel-row number.

Because of the frequent occurrence of the abnormal ear shape in Portuguese germplasm, the author was interested in determining the potential value of the trait for Portuguese breeding programs. To determine the genetics and inheritance of this trait and its relationship with yield, the author brought to the United States a set of 94 Portuguese Regional Varieties (PRVs) collected during 1976 and also during a collection program sponsored by the F.A.O. in 1977. All PRVs had a flint kernel type. From this set of 94 PRVs, 36 were selected to be included in the author's research program at Iowa State University.

The objectives of my study of the Portuguese maize germplasm were:

1. To test for allelism with ramosa (ra1, ra2, and ra3) genes;
2. To test for relative dominance of the abnormal ear trait expression;
3. To study the inheritance and type of gene action involved in the expression of abnormal ear type, because there was a wide range of abnormal ear shapes;
4. To study the potential of the abnormal ear shape and its genetic potential for increasing kernel-row number and its relationship with yield; and
5. To study the heterotic expression of abnormal ear shape in crosses with U.S. Corn Belt germplasm.

II. LITERATURE REVIEW

A. Male vs Female Inflorescence

A general morphologic study of the maize plant was reported by Kiesselbach (1949). In describing tassel formation, he reports that initially both the central axis and branches of the tassel are smooth; outgrowths soon appear, however, which become two-lobed, each lobe finally giving rise to a spikelet with two flowers. In the axil of the lower glume, a growing point forms from which the lower flower is developed. The original growing point of the spikelet gives rise to the upper terminal flower. One stamen in each flower is attached over the middle of the lemma, with a lodicule on either side of the stamen. The other two stamens are attached near the opposite edge of the palea. Each growing point differentiates to form a rudimentary pistil, which, however, does not develop because its growth is arrested and it degenerates and aborts.

In describing the pistillate inflorescence, Kiesselbach (1949) emphasized the similarity between the early stages of both male and female inflorescences except that there are no branches on normal ears. The outer husks are distichous-like ordinary leaves, while the inner are polystichous; sometimes there seemed to be as many ranks of husks as there are double rows of kernels. The ear is initially smooth,

but protuberances soon form in rows. The basal protuberances are formed first and development advances toward the tip of the ear. Each protuberance becomes two-lobed; each lobe develops into a spikelet with two flowers, only one of which commonly persists. Because each spikelet normally produces one kernel, the kernels also will be in double rows and there will be an even number of rows of kernels on the ear.

Although one kernel generally develops for each spikelet to produce an even number of kernel rows on the ear, Hepperly (1949) reported a case of odd-rowed ears.

Nickerson (1954) summarized the research of several investigators and concluded that the maize ear arose phylogenetically by a telescoping and reducing of parts already present in the maize progenitor. From his own investigation, he reported evidence that the female inflorescence was a panicle, many parts of which have been reduced by evolutionary condensation. The massive rachis resulted from telescoping of the primary inflorescence axis and the adnation of prophylls born on secondary or spikelet axes.

It has been established that there are basic similarities between male and female inflorescences in maize. These similarities show a definite point in the physiological growth that some mechanism is responsible for the differentiation of each sex. Both inflorescences initially include

both male and female potentialities, but female aborts in the tassel and male aborts in the ear.

For analyzing the sex reversal often shown in the expression of male or female sex organs in maize, Peterson (1976) observed that these reversals are triggered by adverse environmental conditions and by the activity of numerous genes. To explain the behavior of what he calls "conditional mutants", he proposed that unisexuality in an inflorescence of maize has not come from structural gene changes, duplications or losses, but that such a reduction should be attributed to changes in the regulatory genes that trigger selective abortion of the primordial sex organs in the unisexually developing inflorescence.

East (1910) regarded the maize ear as a fusion of four or more spikes, each joint of the rachis bearing two spikelets. Emerson and East (1913) accepted this concept, but they added another possibility: meristic variations or repetitions of a rachis bearing two spikelets. As DeVries (1899) proposed, East (1910) also concluded that the number of rows per cob seems to exhibit continuous variation. He postulated that number of rows per cob included a series of cumulative units, independent in their inheritance. From the observation that the modal number of kernel rows was always divisible by four, he postulated that through the presence of pure units, zygotes having a multiple of four

rows were formed, while heterozygous units would cause the development of two rows. The eight-rowed maize races would be pure for kernel rows, whereas the twelve-rowed races would vary very little. Races that had a higher number of kernel rows would be exceedingly variable. East (1910) also proposed a theoretical interpretation that can be summarized as follows: (1) assume a basal unit of eight rows to be present in the gamete of all maize races; (2) let additional independent interchangeable units, each allelomorphic to its own absence, account for each additional four rows; and (3) let the heterozygous condition of any unit represent only half of the homozygous condition or two rows. Then, according to his hypothesis, the gametic condition of a homozygous twenty-rowed race would be 8+AABBCC, each letter representing two rows. When crossed, for instance, with an eight-rowed race, the F_2 generation would show ears of from eight to twenty rows, each class being represented by the number of units in the coefficients in the binomial expansion $(a+b)^n$, where the exponent is twice the number of characters or, in this example, $(a+b)^6$. From the results of his studies, East (1910) suggested the following genetic model:

14 rows -- AaBbCc
16 rows -- AABbCc
16 rows -- AaBBCc
16 rows -- AaBbCC

18 rows -- AABBCc
18 rows -- AABbCC
18 rows -- AaBBCC
20 rows -- AABBCC

Anderson (1944) conducted an intensive study of the homologies between the ear and the tassel of maize. He based the importance of such a study on this statement:

> If a corn breeder could size up the potentialities of the ear, merely by examining the tassel, he could take many shortcuts, both in the creation of new inbred lines and in maintaining their desirable characters.

Anderson (1944) studied tassel variation in a general manner for three years before precise correlations of ear and tassel traits were attempted. From his study, Anderson concluded that, in terms of what one human being can accomplish in a lifetime, the number of features of maize ears and tassels which might be measured is almost infinite. He found that the correlations between tassel and ear traits were those which would result if the ear were composed of branches fused spirally about a central cylinder. However, relating tassel profile and shape and size of the ear, he concluded that all patterns are affected by the degree of condensation, which varies independently of the number of tassel branches and their absolute and relative lengths. He defined condensation as a type of controlled fasciation which operates throughout the plant and in the ear as one of the factors controlling kernel-row number. He suggested that the genetic background of condensation seems to be a type of fasciation

due either to a single mutant gene and a large number of minus modifiers or to a large number of genes which produce the same effect. Anderson defined an index CI (condensation index) in this manner: first, the apparent number of tassel nodes is counted and the central three-quarters are selected for computation; second, for the central three-quarters of the tassel, the total number of spikelet pairs in that portion is divided by the number of nodes. This index would also be defined as "the average number of spikelet pairs per apparent node in the most condensed central three-quarters of the basal-most secondary branch of the male inflorescence." He found that for lower values of CI the kernel-row numbers were, on the average, ten times the CI, but for higher values of CI these potentialities were not realized. He suggested, however, that the peculiar conditions of the experiments (three plants per hill) could have contributed to the failure to attain the higher kernel-row numbers. Anderson summarized his evidence for the following ear-tassel correlations:

1. Tassel internode condensation increased kernel row number.
2. Tassel branch length was correlated with ear length.
3. Tassel branch patterns were correlated with ear shape.
4. Tertiary branches were correlated with irregular kernel rows.
5. In North America maize, the relations between tassel condensation and kernel row number were surprisingly exact, according to the formula:

CI = row number/10

Finally, and with the greatest interest for the subject of this dissertation, he found a correspondence between the condensation pattern of the basal-most secondary branches of the tassels and the flattening of the ears. If the tassel branches were highly condensed along its entire length, the ear would be a true "bear-paw". If the tassel branches were highly condensed at the tip, but much less so below, the ear would be more or less circular in cross-section with a flaring two-pointed apex. If the tassel branches were highly condensed at the base, but after that a long uncondensed portion followed, the ear would be broadly elliptic at the base with a normal apex. Anderson emphasized that no exceptions to this generalization were noted in all the materials included for study. It was pointed out, however, that in South American varieties, an increase in kernel-row number was accompanied by an increase of condensation in the central spike, but apparently not in the tassel branches, suggesting more detailed studies were needed to understand the role of fasciation.

Anderson's (1944) conclusions strongly supported the theory that the ear of maize is fasciated. It also seems reasonable that, as a consequence, the ramosa and fasciated types of ears represented lower stages of evolution in the maize ear development. Condensation would be some type of

regular, controlled fasciation, which only occasionally would become so extreme as to produce elliptical axes and multiple growing-points.

White (1948) described two theories regarding the morphological nature of fasciated organs: one, attributed to Moquin-Tandon, defends that fasciation results from flattening or enlargement of a single growing-point; the other, attributed to Linnaeus, hypothesizes that fasciation results from an increase in the number of growth points or buds, and that these, owing to crowding condition, subsequently fuse.

Worsdell (1905), however, favored a modified form of fusion concept, believing that fasciation would result from some sort of compromise between two inherent tendencies and rarely to be a case of real mechanical fusion in the Linnaean sense. Two opposed forces would operate in the organism: one inducing integrity, and the other, inducing plurality of parts. According to this concept, fasciation in higher plants would be regarded as a reversion to the ancestral primitive branching character of the lower plants, such as occurs in ferns, lycopodium, and algae.

B. Ramosa vs Fasciation

The first reference to the ramosa variation in maize was made by Gernert (1912) who described it as Zea ramosa

(from the Latin "ramosus"--many branches) because the ear is "cone-shaped in outline and gives the appearance externally of being composed of a mass of kernels borne on numerous irregular branches." At that time, he believed that this mutant was a new subspecies of Zea mays L.

Ramosa describes an ear in which the simple pistillate inflorescence of maize has been replaced by a compound structure somewhat resembling the tassel (Plate 13). Nearly all the seed is borne on branches; the central axis bears seeds only at the apex. In addition to the branched condition of the ear, the number of branches on the staminate inflorescence has been increased at the expense of the central spike, the latter being reduced greatly in length. The branches of the tassel decrease regularly in length from the base to the tip, giving the tassel a characteristic conical appearance easily distinguishable from the normal form (Plate 12).

Kempton (1921) studied the inheritance of ramosa variation and concluded that it behaved generally as a simple Mendelian character recessive to the normal condition. The characteristic staminate inflorescence always appeared in conjunction with the ramosa ear, enabling him to detect the plants with ramosa ears in the field before examining the ears. From his crosses between the ramosa type and a Mexican maize (which had very few tassel branches and was

called "Gordo"), Kempton found that the Gordo type was completely dominant in the F_1 generation. Influence of the ramosa parent could be detected when the various parts of the inflorescence were measured. In addition, he concluded that ramosa segregates had undergone alterations, and the general appearance of the tassels showed greater variability, which was associated with a similar intermediate condition of the ear. He proposed that the appearance and behavior in inheritance of the intermediate ramosa plants established a relationship with branched forms from nonramosa stocks and furnished evidence for the development of the single-spiked ear through a reduction of branches.

In his treatment of the theme "branched ears", Kempton (1923) postulated five types of ear branching: one included the ramosa type and other a type of branching ranging from one to many four-rowed branches at the base of the ear, usually with fully developed seeds. From studies of this last type of branching, he concluded the trait was inherited in a recessive manner. One of the remaining branched types defined by Kempton (1923) was named "bearsfoot", more frequently reported in the literature as fasciation.

Fasciation had widespread occurrence among vascular plants. Fasciation is commonly referred to as a plant monstrosity or a teratological abnormality. White (1948) reviewed the occurrence of fasciation in plants. After

considering the incidence of fasciation in a large number of crops, including maize, he classified fasciation into five different categories, based on a causal standpoint:

1. Inherited fasciation;
2. Noninherited fasciation due to various environmental causes;
3. Spontaneous fasciation, the initial cause of which is unknown, but which has been propagated vegetatively;
4. Induced fasciation by known artificial procedures;
5. Unclassified fasciation, which has not been investigated experimentally and which remains unknown as to its transmissibility.

According to White (1948), fasciation is a morphological term applied most commonly to an abnormal stem condition in vascular plants. The affected regions became flattened or ribbon-shaped. He postulated instances of fasciation arising as mutations; the progenies inherited the changed condition in an orthodox genetic fashion, and expression was generally associated with modifying genes, which seem to have a large effect on the expression of the fasciation genes. In other instances, fasciated individuals arose from various environmental causes and would not transmit this altered state to their progenies. The basic cause of fasciation, in White's opinion, was the occurrence of disturbed metabolism involving an excess of nutrients. An excess of nutrients mobilized energy that, once accumulated and used in an extravagant manner, caused abnormal and

unpredictable tissue production. Concerning the complexity of the inheritance of fasciation, he stated:

> ...with both the gene-based and the environmentally-caused types of fasciation present in a heterozygous population, with the added complication of modifying gene effects, the difficulty of arriving at the true state of affairs as regards the inheritance of fasciation is easily comprehended.

Galinat (1963) stated that fasciation is a type of incipient branching that flattens the ear and increases the number of kernel rows. He suggested that fasciation had a role in the ancient history of maize, perhaps as a mechanism to concentrate the grain under short protective husks. Galinat (1963) also suggested that genetic factors for fasciation were common in modern maize, but their expression was controlled or modified by teosinte introgression. He also found in the F_2 generation of a cross between "strawberry popcorn" (fasciated) and "Argentine popcorn" (non-fasciated) that, in the absence of teosinte introgression, fasciation segregated as a single factor exhibiting incomplete dominance. For 200 F_2 plants, the segregation ratio was 1:2:1, respectively, of "bear's paw", butt, and normal type. Galinat (1969), however, identified two recessive genes that were involved in the expression of thick-cob type in terms of tassel morphology, in a study of the genetic system of Iowa 5125 (fasciated). One of the recessive genes caused a high condensation in the tassel branches followed by reduced branching; the second recessive gene caused

profuse tassel branching. Galinat suggested that an interaction between the two genes in the double recessive condition would have produced the thick cob and normal tassel of the inbred Iowa 5125. In addition, another genetic system involving a third recessive, operating independently of the high "condensation-ramosa" system, would produce a thick cob in the northern flint derived races.

Orr and Postlethwait (1964) reported that a dominant gene was responsible for the mutation of "fascicled" ear (FA). This fascicled type differed from the normal in that the ear was branched and the tassel had a branched central spike. "FA" plants could be induced to form partially normal ears if treated with indoleacetic acid or α-naphthaleneacetic acid. It is not clear, however, of what fascicled type Orr and Postlethwait (1964) studied and how it related to the ramosa type reported by Kempton (1921) or any of the other four types of branched ears that were described by Kempton (1923).

Daniel (1964) studied the inheritance of fasciation in inbred lines of maize and concluded that for P40 (a popcorn fasciated inbred with an average of 40 kernel rows) the most suitable genetic model would be one that included the following factors:

aa Su-A Su-A bb Su-B Su-B cc dd Su-D Su-D ee ff .

According to his proposed genetic models to explain the different situations, the following genotypes would be

responsible for the fasciation expression:

aa and A Su-A

bb and B Su-B

cc

dd and D Su-D Su-D

ee

ff

EF

Although his approach emphasized the relationship between recessiveness and fasciation expression, it also considered what seems to be a very special situation of two allelic genes (EF). When both allelic genes were in the dominance condition, they inhibited one another and gave a fasciated response.

There is evidence from the literature that there are many instances of inherited fasciation. The most common instances were the monogenic recessive, but dihybrid and trihybrid segregation, with dominant and intermediate inheritance also were reported. Daniel (1964) stated: "Fasciation may behave either as recessive, or as partially dominant, or as a dominant character." In an identical study about the fasciation expression in crosses between maize inbreds with spheroid and flat type ears, Daniel (1973) concluded that the inheritance of the shape of the ear (measured in cross sections of the ear, see Plate 5)

was essentially of additive type. The inheritance of the intensity of fasciation was characterized by dominant effects in a positive direction.

Kato (1970) reported finding some plants with ramosa ears in the Mexican variety 'Yucatan 85'. In his studies, he found evidence of the presence of a dominant gene for that ramosa expression. Because the tassels of those ramosa type plants were, however, of the normal type, he concluded that it was a gene different from ral and ra2. Kato's findings were similar to those reported by Orr and Postlethwait (1964).

From a study of the inheritance of "string cob" trait, Galinat (1971) found the segregation was controlled by two incompletely dominant genes. When studying the correlations of condensation in the tassel and kernel-row number with cob diameter, he found evidence that one of the dominant factors was the normal allele to a recessive gene for fasciation.

In my studies, I found instances of partial dominance and also cases of pseudo-dominant fasciation expression in the F_1 due to the association of recessive genes with suppressor genes.

C. Correlations Among Traits

Emerson and East (1913), in an extensive study of the inheritance of quantitative characters in maize, studied, among other traits, the inheritance of number of kernel rows

per ear, ear length, and diameter. Evidence was presented that number of kernel rows included a series of cumulative unit factors independent in their inheritance. For the differences in behavior shown by races with a low number of kernel rows and races with a high number of kernel rows, they concluded that a portion of such differences was due to correlation with other characters both physiological and gametic. They also reasoned that ears which can vary in any one of eight spikes will show a greater degree of fluctuation than ears which can vary in any one of four spikes. This reasoning would explain why strains with a high number of kernel rows never showed the low variability found in strains with a low number of kernel rows. Their results also suggested that there should be a positive correlation between the dent types and high number of kernel rows.

Emerson and East (1913) also found that the inheritance of ear length was also intimately connected in development and heredity with other ear traits. They found that number of kernel rows was inversely correlated with ear length and was directly correlated with size of the plant. These correlations were ascribed to the physiological component, which can be summarized as: zygote (tall + ear length AABBCC) would give longer ears than zygote (short + ear length AABBCC). They also found reasons to suspect a physiological correlation between long ears and few kernel

rows per ear. When they analyzed the inheritance of ear diameter, they found a direct correlation between diameter and number of kernel rows and seed size. They hypothesized that it was probable that neither seed size nor number of kernel rows of the parents involved differed by as few as two factors, and it would not be unreasonable if the differences in ear diameter were due to as many as seven or eight factors.

Pavličić (1974) studied ten maize cultivars and found that kernel-row number was highly variable; the differences depended on cultivar and year of growth. Ear length depended on genotype and environment and grain length depended more on the genotype. Highly positive correlations were found between ear length and grain number per row, leaf number and days to flowering, and ear length and kernel-row number. Grain number per row and grain length were negatively correlated.

Šatović (1975) studied the components of grain yield at different plant densities at four locations in Croatia. A set of 20,000 ears was examined using path coefficient analysis. Four maize hybrids were included in trials planted at two plant densities (23,200 and 83,300 plants/ha). Šatović concluded that the major factor influencing grain yields was number of kernels per row, followed by average grain weight. Number of kernel rows was of little importance.

Kolčar (1975) studied the effect of urea fertilizer on some ear properties and yield of maize. He concluded that urea and calcium ammonium nitrate increased the number of kernel rows per ear by 5.4% and 4.73%, respectively, compared with no NPK. Khehra et al. (1975), in a path coefficient analysis study of yield components in maize, verified that ear length and girth, kernels per ear, and 1000 seed weight showed positive direct effects on grain yield.

Khristova and Khristova (1976) developed crosses between three maize lines and teosinte (Euchlaena mexicana Schrad.). For ear number, the mean value in the F_1 and F_2 exceeded that of the parents. When the F_1 was crossed with teosinte, the number of ears exceeded that of the multieared parent (teosinte). For ear length and number of kernel rows per ear, the mean value in the F_1 and F_2 also exceeded that of the parents. When the F_1 was crossed with teosinte, ear length and number of kernel rows per ear decreased. When the F_1 was crossed with maize, the mean values of the same characters increased, but did not attain the better parent. The main factors in the inheritance of the multieared trait had additive effects. Inheritance of ear length and number of rows was determined by dominant genes, which tended to reduce the values for these characters.

Mosolov and Chernova (1976) reported a positive correlation between kernel-row number per ear and yield in a

study of maize yield related to nitrogen-potassium nutrition. In potassium (K) experiments, given optimum nitrogen (N) and phosphorus (P) rates, increasing rates of K resulted in increased grain yields by increasing the kernel row number, but no effect was found on plant growth.

Kostyuchenko (1976), however, reported different results in a study of the correlations of productivity with some other traits, in simple and triple hybrids. Grain yield per plant was correlated with average numbers of ears per plant unit area (plants with 0, 1, or $\geq$ 2 ears) and with ear length, but was not correlated with number of kernel rows per ear.

Miranda et al. (1976) studied the environmental effect of different irrigation systems upon maize yields. They found that, for hybrid MA-6, increased irrigation produced significantly higher grain yields and also increased ear length and diameter and leaf area index (LAI). These increases, however, reduced water use efficiency.

Galal et al. (1977) also studied the effects of environment (plant density) upon some ear traits. Trials of the c.v. American Early were conducted at two plant densities: (a) 35,714 plants/ha and (b) 71,428 plants/ha. Ear length, ear diameter, kernel row number, and number of grains per row were greater for 35,714 plants/ha than for 71,428 plants/ha, but the coefficients of variation were

higher at 71,428 plants/ha than for 35,714 plants/ha.

Hussein et al. (1977) studied the effect of preceding winter crops and nitrogen fertilization (0, 74, and 148 kg/ha) on ear characters of maize. Average grain weight per ear in crops following berseem, field beans, barley, wheat, and flax was 142, 131, 129, 125, and 126 g, respectively, with ear length, diameter, and weight following a similar trend. Number of kernel rows per ear was genetically determined and was not affected by treatments.

Ordas and Stucker (1977) included three different plant densities, two locations, and 48 lines of maize to study the genotypic and phenotypic correlations between yield and the yield components number of ears per plant, ear length, and grain depth. Correlation coefficients were 0.45 to 0.81 for ears per plant, 0.29 to 0.71 for ear length, and 0.15 to 0.45 for grain depth. The correlations tended to increase with increased plant density for ears per plant and ear length, but not for grain depth. Generally, the genotypic and phenotypic correlations were of the same order of magnitude. At higher densities predicted gains in yield were 72 to 78% of those measured by direct response when based on ears per plant, and 49 to 72% when based on ear length.

Hansen et al. (1978) compared vegetative and reproductive morphology of maize with grain yield. Total plant dry weight, grain number, ear length, and kernel-row number were

shown to be positively correlated to grain yield per plant, but none of the traits could be used as a sole indicator of yield. Negative relationships were detected between seed weight and grains per row (ear length) with kernel-row number. They suggested a compensating effect of lower seed weight and shorter ear length with increasing kernel-row number.

Schuetz and Mock (1978) studied tassel branch number in maize and its implications for a selection program for small tassel size. They found that additive, dominance, and epistatic gene effects influenced tassel branch number; additive effects were the most important. Additive effects were not significant in two reciprocal crosses involving BSSS 36 and BSSS 78, which were derived from 'Iowa Stiff Stalk Synthetic'. Their results suggested that to obtain a hybrid with small tassels, two inbreds with small tassels and the same alleles for tassel branch number must be crossed.

Romero and Salas (1978) reported that stigma length, cob length, and cob diameter were highly correlated for 10 maize lines.

Galinat (1980) investigated indeterminate vs determinate ears of maize and found that indeterminate ears may elongate under unusually favorable conditions. In contrast, determinate ears occurred in certain strains where consideration for "complete tip fill" tended to conflict with selection for

increased ear length and increased yields. The indeterminate ear trait was largely dominant and was controlled by a factor on chromosome 9 in both Euchlaena and Zea.

Sviridov (1979) studied the heritability of some quantitative characters in maize and found that the coefficients of heritability for plant height, number of grain rows per ear, and ear length were greater for number of grain rows per ear (h^2 = 60%) and plant height (h^2 = 59.9%). Plant height showed overdominance. Ear length had the lowest estimate of heritability (h^2 = 31.1%).

Chernomyz (1979) reported a method of breeding maize for higher grain yield. Good results were obtained when hybrids were formed from parents that had 10 to 12 kernel rows and the other with 18 to 20 kernel rows. He concluded that a good combination of kernel-row number per ear and ear number per plant improved grain yield in inbred lines.

Chuong and Hosokawa (1975) obtained estimates of gene effects for ear length and ear diameter for 10 inbred lines used as parents. Five lines were derived from the same origin and the other five were derived from diverse origins. All possible crosses were made within each of the two groups of five lines. Dominance effects were more important in crosses between lines of diverse origins, while additive effects were of greater importance in crosses between lines of the same origin. The trend was more pronounced for ear

length than for ear diameter.

Cortez-Mendoza (1977) evaluated 10 generations of divergent mass selection for ear length in 'Iowa Long Ear Synthetic'. He used the biparental or Design I mating design and found that additive genetic variance accounted for all the genetic variance for yield, ear length, ear diameter, kernel-row number, and 300-seed weight. Dominance effects were important for silking date and ear length. Genotypic correlations and heritability estimates were low in all instances. In a further study of the same experiments, Cortez-Mendoza and Hallauer (1979) reported that the predicted and actual responses for increased ear length were nearly the same, but the actual response for decreased ear length was twice as great as that for increased ear length, suggesting that unequal gene frequencies and directional dominance of genes affecting ear length were responsible for the asymmetry observed. The correlated responses of grain yield per plant, ear diameter, kernel length, ear height, and number of days to silking were also asymmetrical. Selection for increased ear length was not accompanied by a correlated increase in grain yield per plant, but selection for decreased ear length was accompanied by a significant correlated decrease in grain yield per plant. They concluded that selection for increased ear length was not effective in promoting increased yield.

Hallauer and Miranda (1981) summarized data from the literature for 20 different traits of maize. Data showed that dominance seemed important in the expression of yield and the heritability estimate on a plot basis was low (18.7%). For the traits ear length, ear diameter, and kernel-row number, the additive component of variance was of greater importance. Heritability estimates for ear length and ear diameter were relatively low (38.1% and 36.1%, respectively), but heritability for kernel-row number was relatively high (57%). In an identical summary of data concerning the Iowa Stiff Stalk Synthetic, they reported that estimates of heritability on a plot basis for yield, ear length, and ear diameter were 24.8%, 37.8%, and 29.5%, respectively. They also summarized the correlations among plant and ear traits with yield by averaging the values reported in the literature. The correlations between yield and ear length, ear diameter, and kernel-row number were 0.38, 0.41, and 0.24, respectively. Correlations between ear diameter and ear length, and between kernel-row number and ear length were small negative values (-0.01 and -0.16, respectively). A significant positive correlation also was reported for kernel-row number and ear diameter (0.57). In a similar summary for the Iowa Stiff Stalk Synthetic, the following correlations were obtained between yield and ear length, ear diameter, and kernel-row number: 0.45, 0.54, and 0.45,

respectively. Correlations between ear diameter and ear length were low (0.03) as well as between ear length and kernel-row number (0.19). But the correlations were high between kernel-row number and ear diameter (0.70), and between kernel-row number and kernel depth (0.60).

D. Germplasm Potential

Germplasm collection, evaluation, preservation, and utilization have received greater attention in recent years from biologists and plant breeders as well as from international institutions and governments. One reason for the increased awareness of the fundamental value of germplasm is because germplasm is a major source to assist in the food challenge for an increasing population growth.

Duvick (1981) discussed how new pests have attacked specific crop varieties and have spread explosively and unexpectedly, giving rise to disastrous nation-wide epidemics and infestations. Some specific examples included the epidemic which caused the potato famine in Ireland in the 1840s, the stem rust epidemics in wheat, and the 1970 epidemic of southern corn leaf blight (Helminthosporium maydis L.), race T; each of these epidemics was responsible for big yield losses. In the discussion of maize breeding methods for the 21st century, Duvick (1981) based his reasoning on a balanced pattern of "genetic vulnerability"

versus "genetic diversity". He emphasized the importance of two related factors: genetic diversity in time and genetic diversity on the farm. The first factor will be achieved by planting new, different varieties every few years, and the second factor by planting several unrelated varieties or hybrids. He stated that, on the average, hybrids in the United States were replaced every seven years and that inbreds lines also have a relatively rapid turnover rate, which was about 10 years of major use per line. Nevertheless, Duvick also stated that presently only about 5% of the diversity in Zea mays L. is utilized, and emphasized that we must continue to diversify our breeding materials to increase the diversity among hybrids growing on the farms. We should remember, however, that Duvick's concepts of "diversity in time" and "diversity on the farm" are especially applicable to advanced agriculture systems such as those used in the United States.

Hallauer and Malithano (1976), from a study of evaluation of maize varieties for their potential as breeding populations, suggested that exotic germplasm should receive greater attention. In his studies involving BS 16, developed from the Colombian 'ETO composite' by six cycles of mass selection for early silking, and BS 2, developed by intercrossing the ETO composite with six early lines and random mating for five generations, he concluded that the line with 100%

exotic germplasm (BS 16) was superior. In a discussion of the use of exotic germplasm, Hallauer and Miranda (1981) emphasized five important points: (1) most of the evidence reported from use of exotic with adapted germplasm has been encouraging; (2) useful genes in exotic germplasm will not be available until they are incorporated with the highly productive adapted germplasm; (3) the initiation of selfing in recently hybridized exotic-adapted germplasm has been disastrous because of severe inbreeding depression; (4) a common error was not recombining the best progenies and initiating another cycle of recombination of the best material; and (5) immediate payoffs are not to be expected, but long-range payoffs seem likely.

A general view of germplasm potentials was given by Kuleshov (1933) in a perspective about the "world's diversity of phenotypes of maize." Using a broad maize collection stored at the Institute of Plant Industry in Leningrad, USSR, Kuleshov found maize to have an extraordinary diversity of morphological and biological characteristics. This diversity among maize collections explained the extraordinary large area occupied in the world by Zea mays L. Maize is grown from 57° to 58° latitude north to 35° to 40° latitude south. Maize is grown in a range of altitudes from the Caspian plains (below sea level) up to 3,000 meters in the Andes (Peru); from the arid and semi-arid plains of USSR

with only 250 mm of yearly rainfall to the tropics of Hindustani with 5,000 to 6,000 mm of precipitation; from the short summer in Canada to the continuous growing seasons of tropical Colombia. Examples of the range of variation for different traits of maize would include:

(1) Height of the plant (60 to 700 cm);

(2) Number of leaves on the principal stalk (8 to 48);

(3) Leaf length (30 to 152 cm);

(4) Leaf breadth (4 to 15 cm); and

(5) Number of stalks (1 to 12).

Considering the biology of flowering, an interesting case was described. In most of the European and North American varieties, there was an effect of protandry which was still more evident in samples from the tropical zones in America. The opposite was found in many of the samples from large regions of Central Asia with simultaneous flowering and sometimes even protogyny occurring. Another interesting situation was related with plant height. Generally, plant height was related with length of the growing season. But many samples from mid-Asia, only 100 to 120 cm tall, were found to ripen just as early as the American varieties, 'Krug' and 'Leaming', which were 250 to 270 cm tall. Considering the potential of flint types, Kuleshov (1933) found that, in a test of earliness, all the extra-early varieties were flint types. He emphasized that in the Old World the

flint type was of exceptional importance. From the coasts of Portugal and Spain to the coasts of the Pacific and also in Japan and neighboring islands, the flint types were predominant. In the northern frontiers of maize cultivation, the flint varieties were predominant, but as we proceed southward their importance decreases. This finding could be connected with the areas where Columbus and his followers landed, where flint types were grown almost exclusively. Finally, Kuleshov (1933) concluded there was almost a complete absence of study upon the extra-late maize varieties. Kempton (1924) stated:

> To be of maximum efficiency, plant breeding must deal with all existing wild relatives of the plant being bred, for it is only in this way that investigators can take advantage of special characteristics acquired through ages of evolutionary progress.

Galinat (1963) found experimental evidence indicating that genetic factors for fasciation were common in modern maize, but their expression was controlled or modified by teosinte introgression. He reported that his teosinte chromosome 9 stocks caused complete submersion of any phenotypic effects of heterozygous fasciation in its hybrids with 'Strawberry popcorn' (fasciated), and with a fasciated sweet corn inbred Iowa 5125. All teosinte chromosomes tested (1, 3, 4) caused some reduction in both fasciation and kernel-row number as well as an increase in ear length in such hybrids. Galinat (1968) postulated that the

fasciated inbred, Iowa 5125, should have a low level of teosinte introgression because this is known to reduce or eliminate fasciation.

Galinat (1973) suggested a method for obtaining giant ears of maize as a result of his own studies using teosinte chromosome 9. Such a method would include the five following steps:

1. Heterozygosity for teosinte chromosome 9, since a factor on this chromosome elongates the rachis internodes in the upper half of the ear and thereby eliminates a fasciated tip by allowing interlocking cupules and spikelets.
2. Homozygosity for fasciation of the ear. This causes the cob to be highly vascularized at its base.
3. A single main ear borne low in the stalk.
4. A tall (2.70 to 3.00 m) late flowering plant with tillers.
5. A long central spike in the tassel.

Considering this kind of germplasm a rarity, Galinat (1963) wrote:

> Although obvious fasciation is rare in modern maize, it does occur in extreme form in certain relic races, which are now restricted to high elevations such as 'Palomero Toluqueno' in Mexico and 'Confite Puneno' in Peru, as well as in a case which is maintained as a novelty type in the United States, Strawberry popcorn.

This dissertation includes evidence that these types are not only present in the high elevations of Central America, but also in the lowlands of the Portuguese coast where these "relics" can be found.

Maize was totally unknown in Europe and Asia until the arrival of Columbus in the New World in November of 1492. Columbus discovered on the island of Cuba great fields of the strange new plant, which was later found to be cultivated throughout the Western Hemisphere.

Brandolini (1970), in his work about the European maize races, discussed the diffusion of maize in Europe, when first introduced in the south in the first half of the 16th century. In the second half of the 17th century, maize was already introduced in all of Southern Europe. During the 18th century, new, very early flowering varieties were introduced in the European continent from the French and British colonies of Canada and New England. Finally, the last major introduction of maize in Europe occurred during the last decade of the 19th century. Whereas the first introductions to Europe were of the flint type, the last introductions were of the dent type, which contributed to greater yields and consequent greater expansion of maize acreage. He reported similarities among the maize germplasms from Italy, Morocco, and Portugal, and the high combining ability between European and U.S. Corn Belt inbreds.

Costa-Rodrigues (1969) included a set of 163 maize samples to study the Portuguese races of maize. He emphasized that such basic material was far less than needed to assure a thorough survey of the races of Portugal. Although Portugal was a relatively small country, there was great variation in maturity of Portuguese varieties, ranging, according to the FAO classification, from 100 to 1000. Variation was influenced mainly by the temperature distribution, by the possibility of planting maize from February to July, under dry-farming or irrigation, and by harvesting from July to late October according to locations and particular conditions of the crop. He found that Portuguese maize could be divided into 10 races:

(1) Race microsperma (M);

(2) Race crossed microsperma (XM);

(3) Race eight rows (8 r);

(4) Race conical eight rows crossing (C x 8);

(5) Race small conico (Cp);

(6) Race crossed conico (X C);

(7) Race conico (C);

(8) Race big conico (Cg);

(9) Race large eared (CN); and

(10) Race gigantil (A).

Since the first introductions of maize in Portugal were believed to have been made by the Portuguese sailors who

accompanied Columbus on his second trip, maize has been in Portugal for five centuries under several different selection pressures. He found evidence relating races Microsperma, Crossed Microsperma, Eight Rows, Conico Eight Rows Crossing, Crossed Conico, Conico and Big Conico with the Early Caribbean race; and races Large Eared and Gigantil could be related to the Coastal Tropical Flint or Cuban Flint races. Finally, by observing the diagram of distribution of mean racial values of tassel peduncle length and total internode length, he suggested that the present races of maize in Portugal originated from a restricted number of races of the Western Hemisphere. Selection for earliness has evolved new races to fit the microclimatic conditions of Portugal. The characteristics of the basic genetic materials included in this dissertation did not permit including PRV 30 in any of the races described by Costa-Rodrigues.

III. MATERIALS AND METHODS

A. Materials

A set of 94 open-pollinated Portuguese Regional Varieties (PRVs) was brought to the United States by the author as the basic genetic material for his research. Among the PRVs some included a very high percentage of ears with abnormal shape, which would constitute the principal subject of this dissertation.

From the original set, three subsets of 12 PRVs each were chosen using the following criteria: (1) division of the Portuguese traditional maize growing area into three regions (Figure 1) and (2) percentage of abnormal ears within the PRVs for each area. The chosen areas are identified as the Districts of Viana do Castelo (region 1), Porto (region 2), and Leiria-Coimbra (region 3). Germplasm from region 1 is roughly characterized by short, leafy plants adapted to very low lands that are near sea level and include some salty soils. In region 2, maize is grown along the valleys from low to medium altitudes (100-600 m) and plants are generally tall with high ear placement. Region 3 represents the lowlands along the Atlantic coast with the exception of PRV 74, which is grown at 600 meters altitude from the coast to the mountains in the east. The relative location of the regions is given in Figure 1. Additional data describing the three subsets of PRVs are presented in Table 1.

Figure 1. Location of three regions of Portugal from which the maize germplasm included in my study was collected

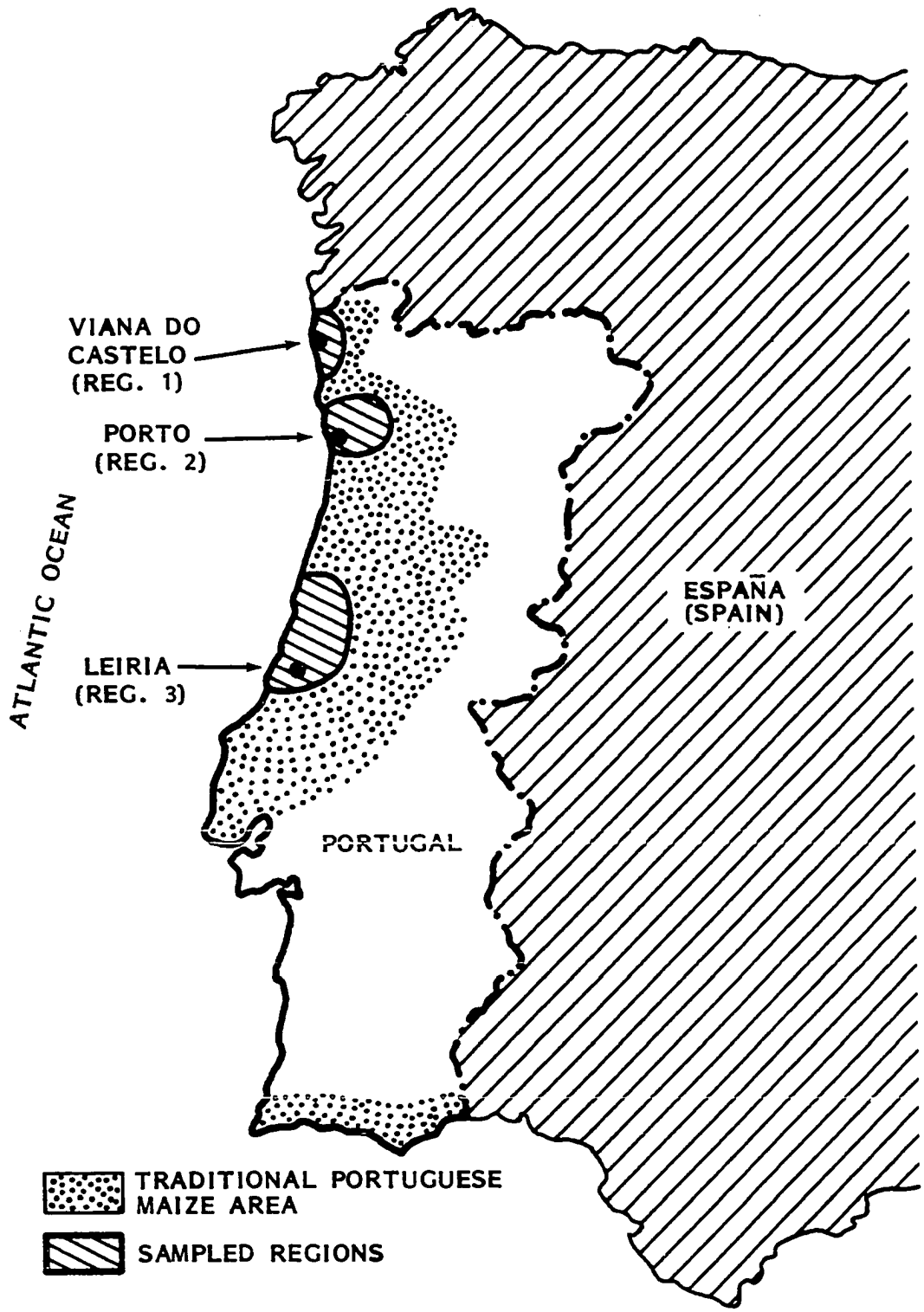

VIANA DO CASTELO (REG. 1)
PORTO (REG. 2)
LEIRIA (REG. 3)
ATLANTIC OCEAN
ESPAÑA (SPAIN)
PORTUGAL
TRADITIONAL PORTUGUESE MAIZE AREA
SAMPLED REGIONS

Table 1. Identification data for the 36 Portuguese Regional Varieties (PRVs) collected in the three regions of Portugal

PRV #	Common name	District	County	Village	Alt. (m)	Irri-gation	Year col.
			Region 1				
18	Amarelo	V. Castelo	Cerveira	Breia	100	Yes	1976
214	-	"	Viana	-	5	No	1977
216	Milho de folha	"	"	Montedor	5	Partial	1977
217	-	"	"	"	5	Yes	1977
220	-	"	Âncora	Lage	20	Yes	1977
221	-	"	"	"	50	Yes	1977
223	-	"	"	"	20	Partial	1977
224	Meia palha	"	"	"	5	No	1977
225	Amarelo	"	Caminha	Gontinhais	5	No	1977
230	-	"	"	Vanada	3	Yes	1977
233	Mulato	"	"	Seixas	60	No	1977
255	Amarelo	"	Viana	Subportela	80	Yes	1977
			Region 2				
23	Milho de cunha	Porto	Gondomar	Foz do Sousa	-	Yes	1977
25	Regional	"	P. Varzim	Terroso	50	Yes	1976
28	Milho bravo	"	Sto Tirso	Trofa	-	Yes	1976
29	Temporão	"	"	"	-	Yes	1976
30	Chato	"	Valongo	Alfena	-	Yes	1976
161	-	"	Penafiel	Penafiel	190	Yes	1977
163	-	"	M.Canavezes	Entre Rios	40	Yes	1977
171	-	"	Baião	Ponte Gouva	380	Yes	1977
183	-	"	Penafiel	Mudelos	200	Yes	1977
184	-	"	"	"	200	Yes	1977
185	-	"	"	"	200	Yes	1977
191	Palha alta	"	Maia	Águas Santas	30	Yes	1977

Table 1. (Continued)

PRV #	Common name	District	County	Village	Alt. (m)	Irri-gation	Year col.
			Region 3				
37	-	Leiria	Pombal	-	-	Yes	1976
38	-	"	"	Louriçal	40	Yes	1977
39	-	"	"	"	80	No	1977
62	Pego	"	Leiria	Arrabal	170	No	1977
63	Regional	"	"	Amor	40	Partial	1977
66	-	"	"	Coimbrão	50	Yes	1977
74	Meia palha	"	Pedrógão	Graça	600	Yes	1977
99	Meia palha	Coimbra	Cantanhede	Mira	30	No	1977
100	Palha baixa	"	Mealhada	Leitões	30	Yes	1977
101	Palha baixa	"	Mira	Mira	10	Yes	1977
103	Verdial	"	Cantanhede	Tocha	60	Yes	1977
110	Boca de sapo	"	Coimbra	S.M.Amares	20	Yes	1977

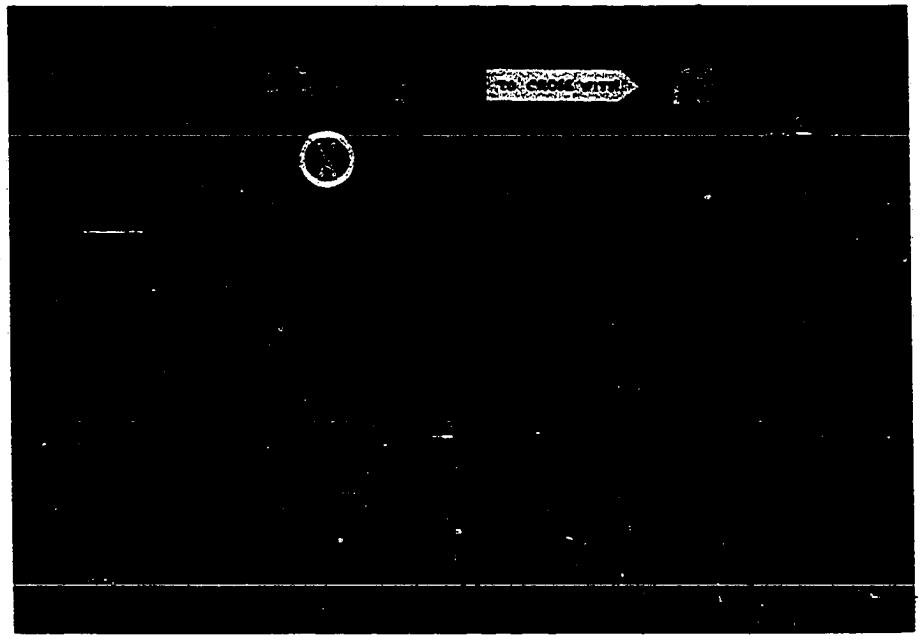
Because the abnormal shape of the ear is characterized by a flat ear type (Plates 1 to 5) which generally is wider at the top than at the base (a strong fasciation sometimes approaching the ramosa 1 type), it was hypothesized that the ear shape was caused by a gene allelic with ramosa genes, specifically with ra1. Furthermore, because two PRVs (PRV 30 and PRV 38) collected in 1976 had the abnormal ear shape present in more than 90% of the ears collected (Plates 3 and 4), the possibility also was considered that a dominant gene might be responsible for the trait. Hence, a qualitative genetics approach was designed to test whether a single dominant gene or an allele of the ramosa genes was causing the abnormal ear shape. Genetic stocks that included the ra1, ra2 and ra3 genes were crossed with the selected PRVs according to the following sequence:

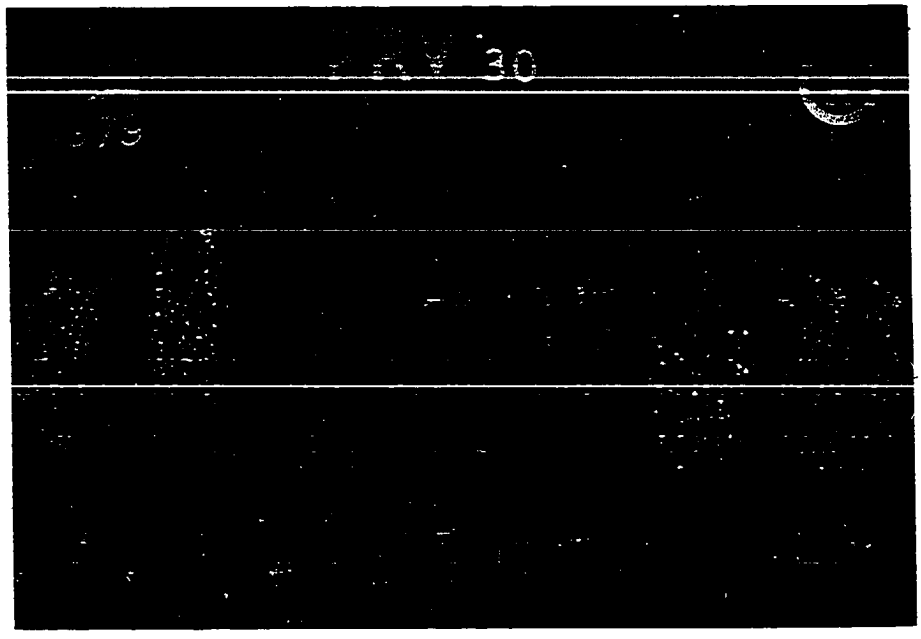
$$\text{PRV} \times \begin{matrix} \underline{ra1} \\ \underline{ra2} \\ \underline{ra3} \end{matrix}$$

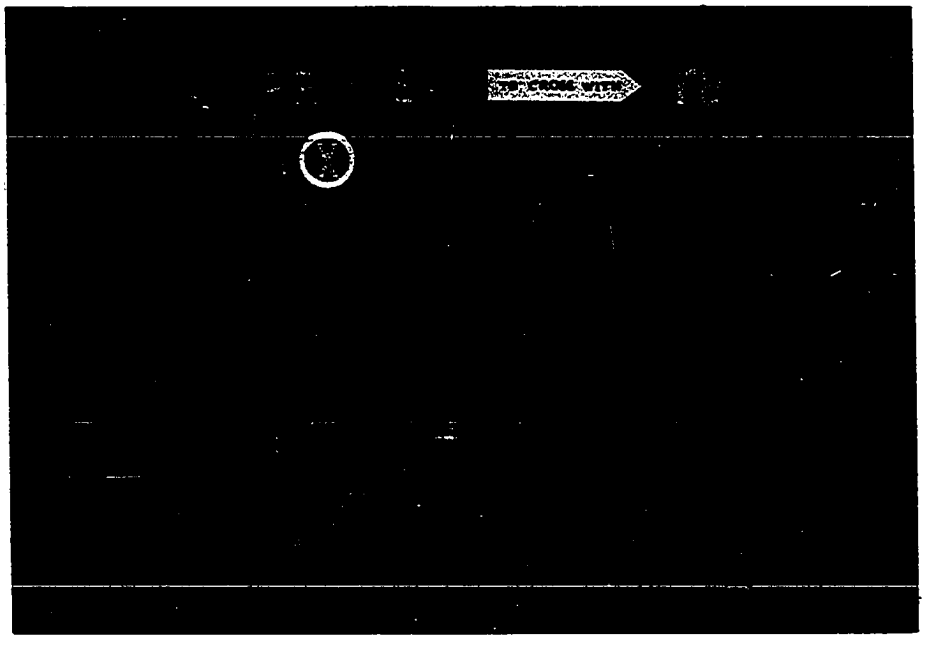
If allelic to one of the genetic stocks, they would all be ramosa; if different gene, all ears would be normal; and if dominant gene, all ears would be ramosa for all genetic stocks. To test the possible alternatives, the following genetic materials were used: (1) genetic stocks that included the ramosa genes (ra1, ra2 and ra3), which were obtained from Maize Genetics Cooperative in the heterozygous condition; (2) the 36 PRVs collected in Portugal;

Plate 2. A set of ears representing several PRVs covering a wide range of fasciation expression

Plate 3. A sample of selfed ears from PRV 30







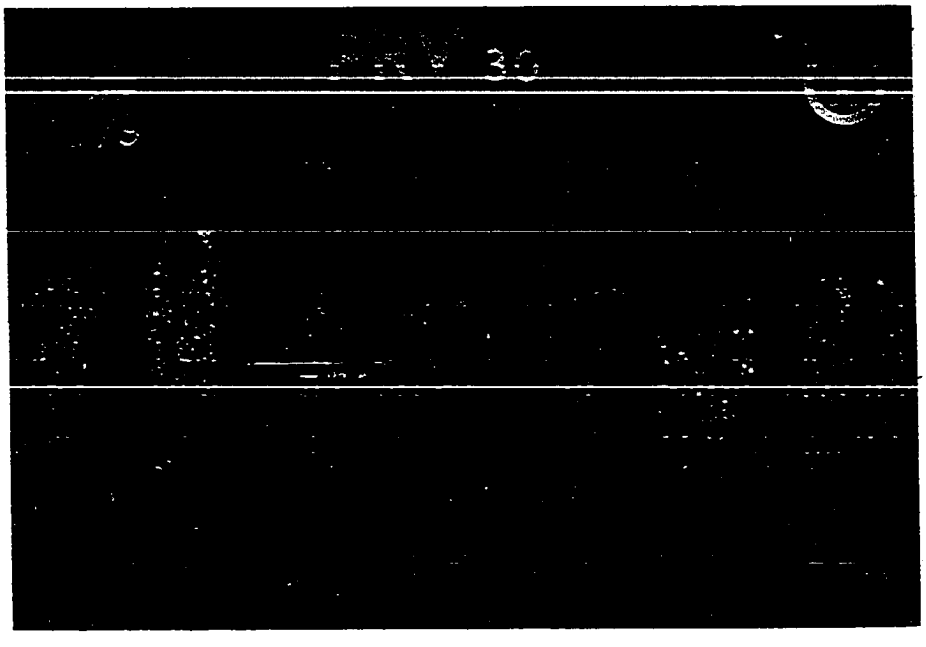
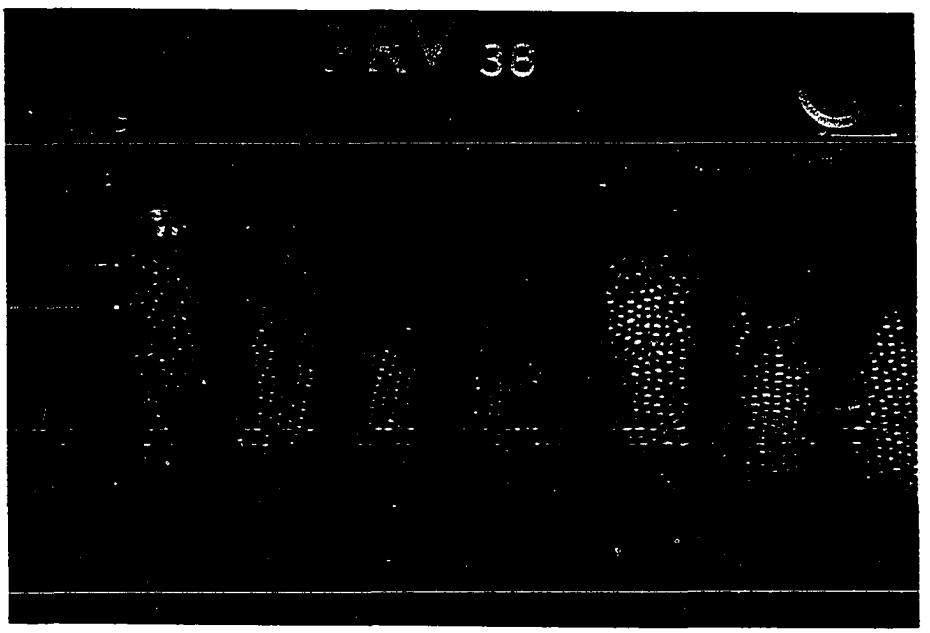
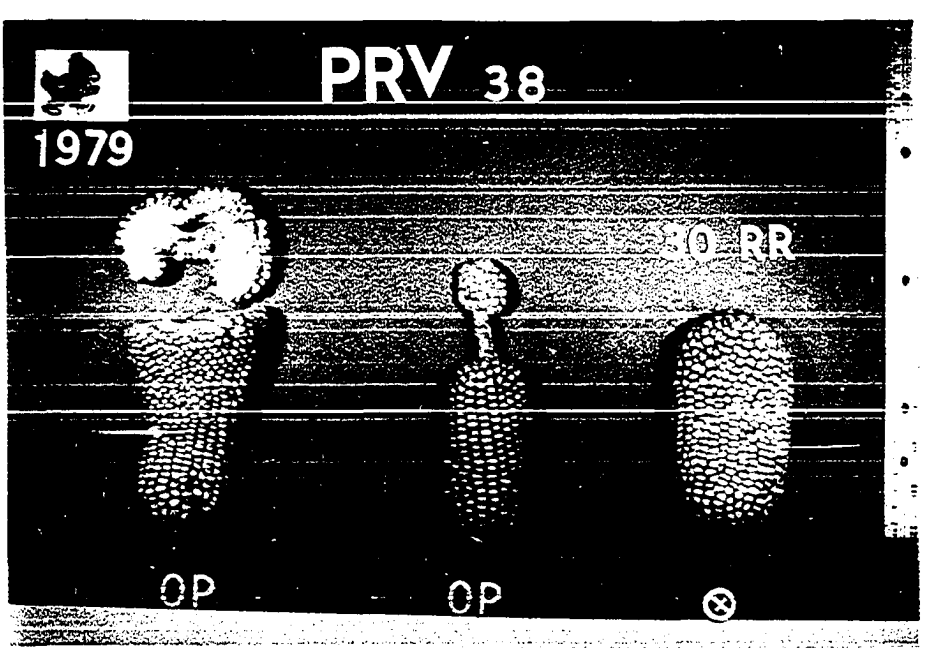


Plate 4. A sample of ears representing PRV 38

Plate 5. Different levels of fasciation expression found in PRV 38; ear on left shows a transversal section




PRV 38
1979
OP
OP

and (3) four inbred parents of a Portuguese double-cross hybrid in which the abnormal ear character was incorporated.

B. Procedures

During the summer of 1979 at the Agronomy Farm near Ames, Iowa, the genetic materials were grown in four-row plots. At flowering time, a random sampling was made in the PRVs for ear development in order to select the degree and percentage of abnormal ears within each PRV. As a result of this 1979 sampling, it was possible to reduce the initial number of PRVs from 36 to 6. The six selected PRVs and regions of collection are as follows:

Region 1 - PRV 214, PRV 216

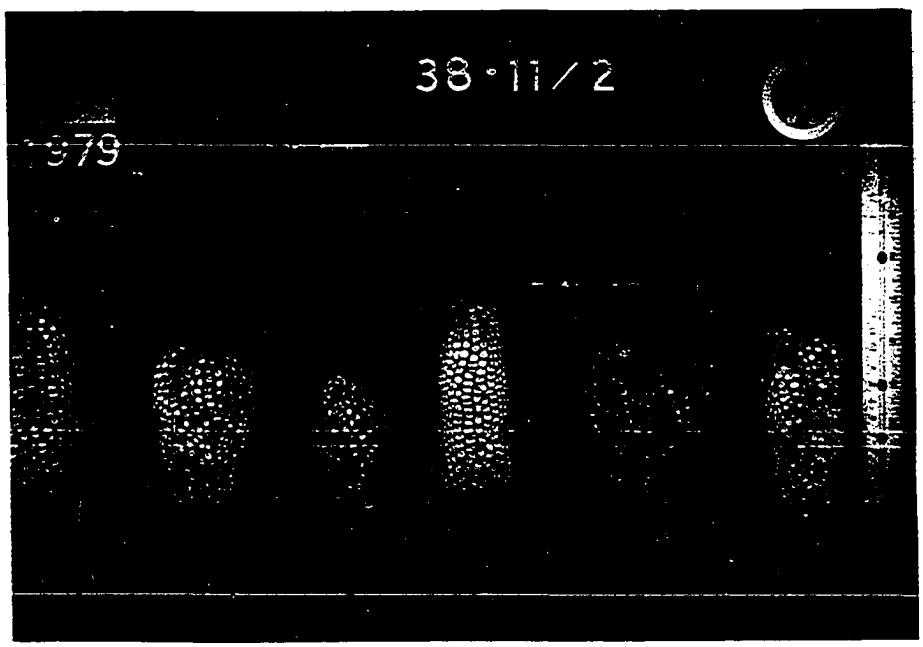
Region 2 - PRV 30

Region 3 - PRV 38, PRV 99, PRV 37

Individual plants from these six PRVs were crossed as males with plants of the three ramosa sources (ra1, ra2 and ra3), and each male plant also was selfed. The remaining plants within each PRV were sib-mated. The same procedure was followed with the two inbred parents (Plate 7) of the female single cross of the Portuguese double-cross hybrid HB 19 (WF9R x 38-11/2) x (33-16R x PB 103) (Plates 8 and 10). The reason for including the two inbreds was because the inbreds WF9R and 38-11/2 were modified white versions of the old U.S. inbreds and possessed, to a certain degree, the

Plate 6. A sample representing inbred 38-11/2 showing the variation for fasciation expression in an inbred with advanced generations of selfing

Plate 7. The pedigree (inbred parents) of the Portuguese double-cross hybrid HB 19


38·11/2
379

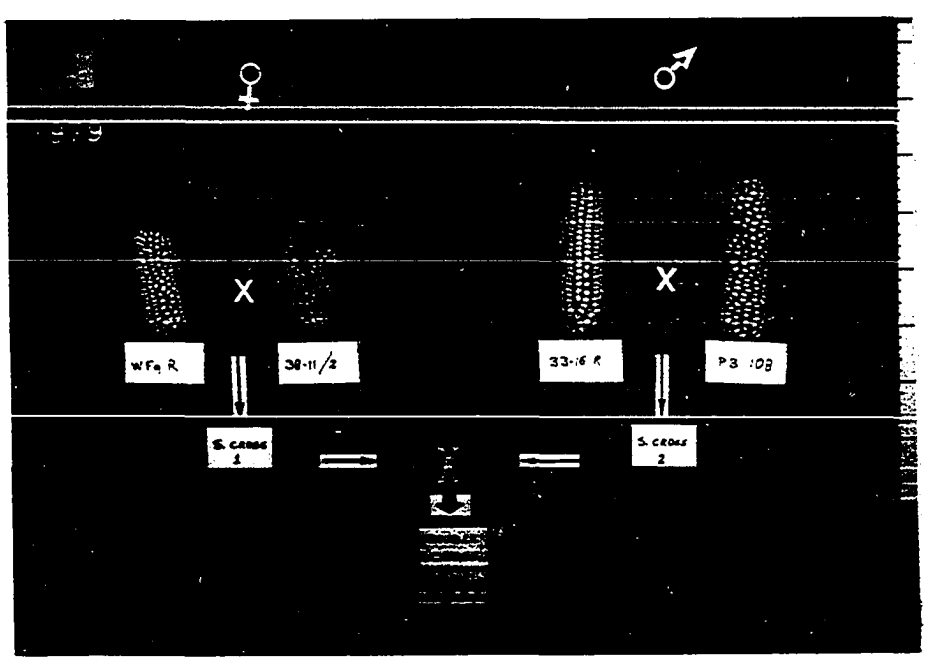
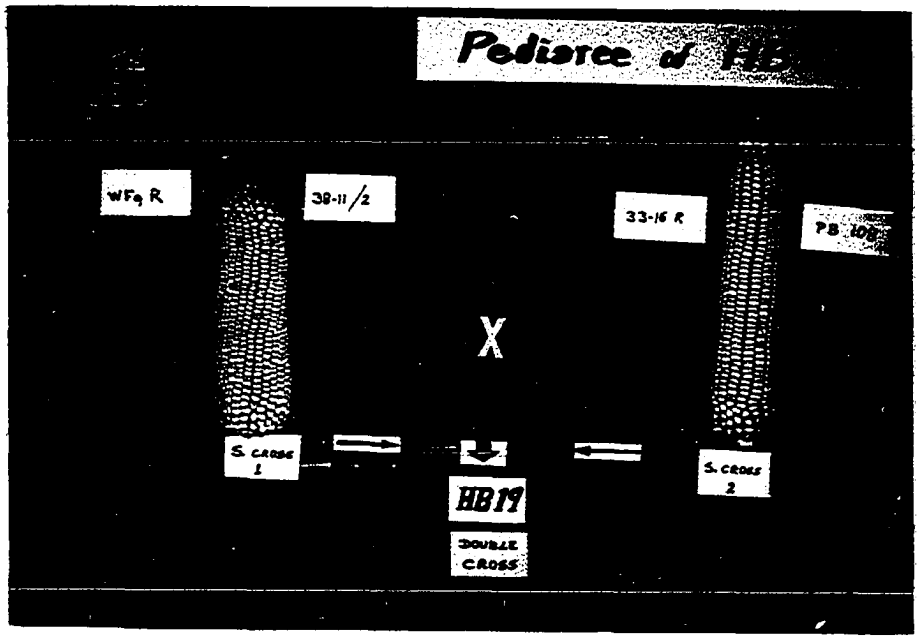

♀
♂
X
X
WFa R
38-11/2
33-16 R
P3 108
S. cross 1
S. cross 2

Plate 8. Pedigree (single crosses) of the Portuguese double-cross hybrid HB 19

Plate 9. A sample representing the female single-cross (WF9-R x 38-11/2) of the Portuguese double-cross hybrid HB 19 showing the uniformity for fasication expression


Pedigree of F1
WF9 R
38-11/2
33-16 R
X
S. CROSS 1
S. CROSS 2
HB19
DOUBLE CROSS

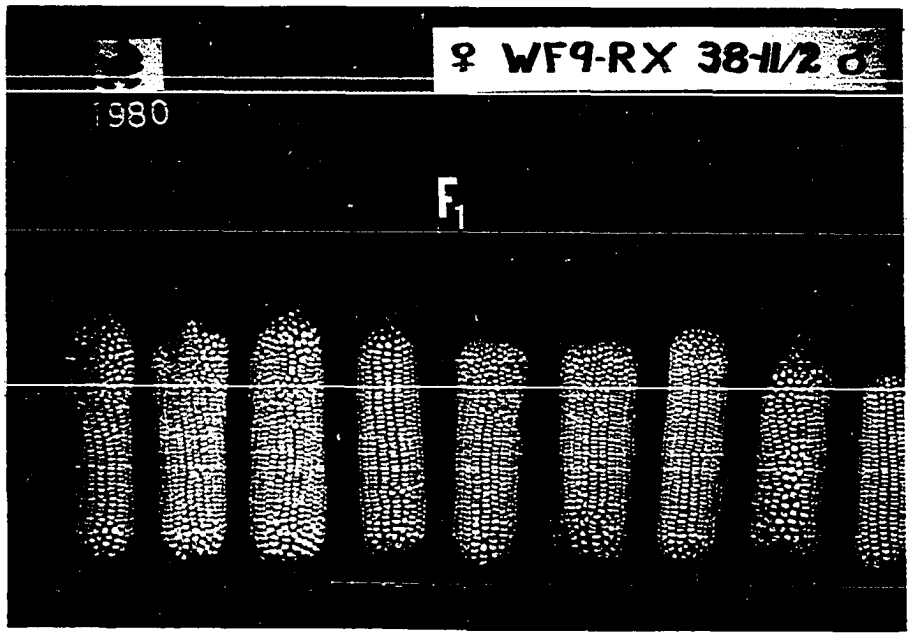
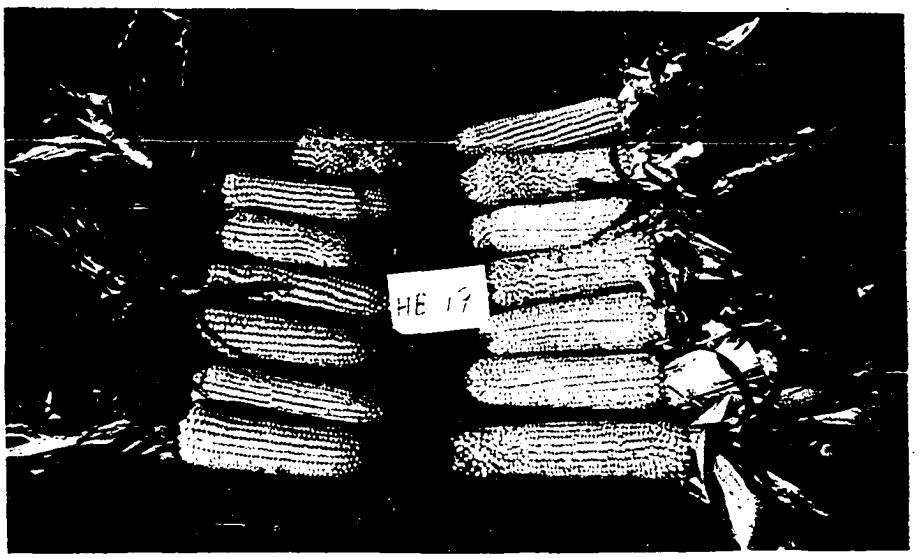

♀ WF9-RX 38-11/2 ♂
1980
F1

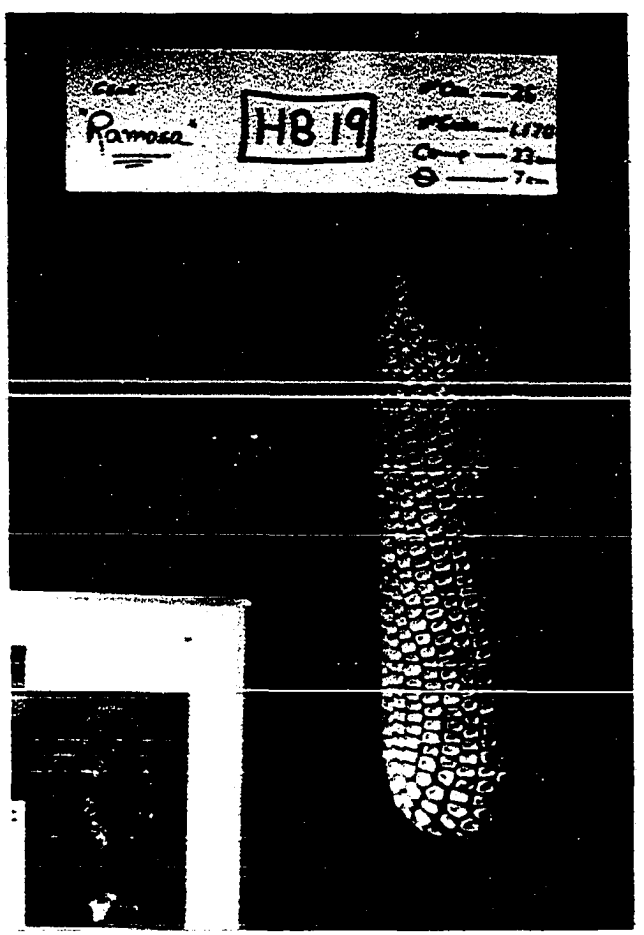
Plate 10. A sample representing the Portuguese double-cross hybrid HB19 as grown in northern Portugual

Plate 11. An ideotype ear of the Portuguese double-cross hybrid HB19; this ear showed the following characteristics:

Ear length, 23 cm
Kernel-row number, 26
Kernel depth, 15 mm
Middle diameter, 7 cm
Total number of kernels, 1170

In the left corner, a picture of ramosa 1 (ra1ra1) ear phenotype from "The Mutants of Maize" (Neuffer, Jones and Zuber, 1968)


HE 17

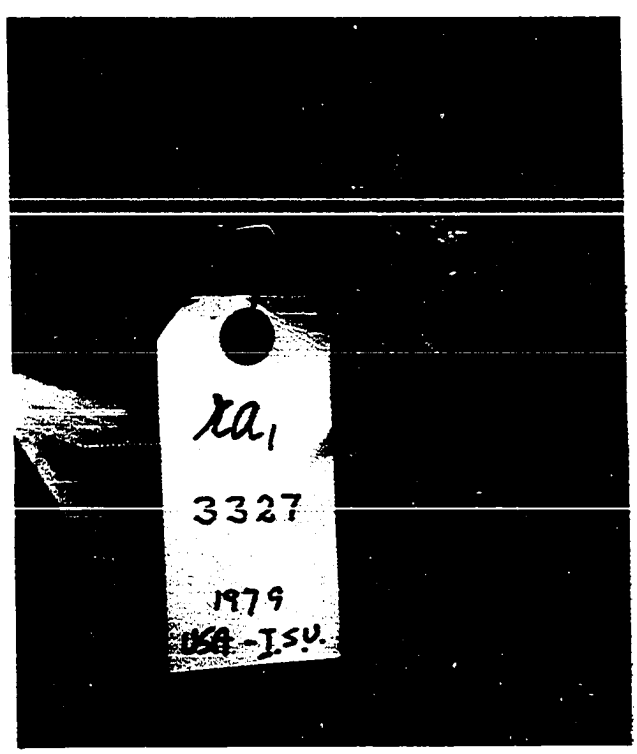

Ramosa
HB 19

character under study. The expression of abnormal ear shape in the two inbreds occurred because of previous crosses with this type of Portuguese germplasm followed by several backcrosses to the recurrent parents.

Due to natural difficulties of different flowering periods, some male plants were crossed with more than one female, but the majority of the crosses involved different male and female plants. The most important barrier to making all the desired crosses occurred with the ral source. Because homozygous plants are easily identifiable due to the conic shape of the ral tassel, we attempted to use only the homozygous plants (ralral) in the crosses with the different PRVs. However, it was found, because of late flowering of the female inflorescence (there was about a week interval between male and female inflorescences), very few homozygous plants could be used in the crosses. The homozygous ralral plants also were highly susceptible to corn smut (Ustillago maydis L.) (Plate 13). Most of the crosses with ralral, consequently, were not successful. For these reasons, almost all crosses involving the ral source included heterozygous plants as females. All plants included in the crosses were numbered, and the crosses were identified by the respective pedigrees containing plant number of male and female. A small amount of seed of the single-crosses of double-cross hybrid HB 19 was also produced by hand pollination.

Plate 12. Comparison between the tassel phenotypes of an homozygous plant for ramosa 1 gene (ralral) and of a normal plant; ramosa tassel at left and normal tassel at right

Plate 13. Phenotypic ear expression of a plant homozygous for ramosa 1 gene (ralral) in early stages of development


Xa1
3327
1979
USA-ISU.

At harvest, all the selfed and crossed ears were collected as well as all the PRVs (selected and unselected). In each unselected PRV, two sets of ears were formed: the sibbed and the open-pollinated ears. All the ears were counted and visually classified for fasciation expression in three categories: fasciated (F), normal (N), and intermediate (I). The fasciated classification was a phenotypic expression of all ears that had a consistent flat type shape at the top of the ear. The intermediate expression was characterized by a position between the normal and the fasciated types. This first classification was appropriate to give a first evaluation of fasciation expression within each PRV. After this evaluation (see Table 2), the open-pollinated ears were discarded. The sibbed ears were shelled, the seed bulked, and seed sample of each PRV was given to the North Central Regional Plant Introduction Station at Ames for its maize germplasm bank. A sample of each PRV was photographed for germplasm data collection (Plate 3).

The selfed plants, which functioned as males in the crosses with ramosa genetic sources, were shelled (S_1 seed) and prepared for the next growing season. The crossed plants used as females were also shelled (F_1 seed) and sent to a winter nursery in Florida. Before shelling and for each cross, a photograph was made for both ears, representing

Table 2. Expressivity of abnormal shape of ear (fasciation expression) among the three sets of PRVs expressed as percentage of fasciation over the total (F/E)

Region	PRV #	Normal shape (N)	Inter-mediate shape (I)	Abnormal shape (F)	Total # of ears (E)	F/E %
1	18	84	0	0	84	0
	214	18	18	16	52	31
	216	30	12	7	49	14
	217	76	2	0	78	0
	220	78	5	5	88	6
	221	75	0	0	75	0
	223	73	1	1	75	1
	224	84	7	6	97	6
	225	55	3	3	61	5
	230	66	0	0	66	0
	233	101	0	1	102	1
	255	117	1	0	118	0
2	23	27	0	0	27	0
	25	69	0	1	70	1
	28	74	0	0	74	0
	29	56	0	6	62	10
	30	0	2	25	27	93
	161	102	0	0	102	0
	163	62	3	3	68	4
	171	101	0	1	102	1
	183	64	0	1	65	2
	184	60	2	1	63	2
	185	4	0	0	4	0
	191	38	16	18	72	25
3	37	5	8	43	56	77
	38	3	6	22	31	71
	39	28	11	7	46	15
	62	67	2	2	71	3
	63	62	0	0	62	0
	66	73	2	0	75	0
	74	53	3	1	57	2
	99	7	13	36	56	64
	100	64	0	0	64	0
	101	62	4	0	66	0
	103	84	0	0	84	0
	110	26	21	22	69	32

the female and male plants involved (Plates 16 and 23).

During the winter of 1979-80, the F_1 plants were grown and selfed in Florida to obtain the S_0 or F_2 seed. The selfed plants were harvested and the ears brought to Ames where they were classified for fasciation expression, and a photographic coverage of all entries was made (Plates 18 and 25).

Because of the natural difficulty in obtaining crosses with the homozygous ral/ral plants during the summer of 1979, it was intended to repeat some crosses using the homozygous plants as males. This was made also in the winter of 1979-80 in the greenhouse at Ames. Two rows of heterozygous (+/ral) plants were sown at two different dates to cover the flowering times of the females. The seed used to produce the females was S_1 seed from plants used as males during the summer of 1979. The following set of one-row plot females was crossed with ral/ral plants in the greenhouse:

PRV 30-71
PRV 37-17
PRV 38-88
PRV 99-89
PRV 214-100
PRV 216-101
WF9R
38-11/2

At flowering time, the heterozygous ramosa (+/ral) plants were eliminated and only the homozygous (ral/ral) plants were used in the crosses. The crosses produced in the greenhouse were intended to substitute for those that failed in 1979.

Plate 14. Comparison between a tassel from a homozygous plant for ramosa 1 gene (ra1ra1) and a homozygous plant for ramosa 2 gene (ra2ra2); ramosa 1 tassel at left and ramosa 2 tassel at right

Plate 15. An ear of PRV 39 (S_1) representing a case of transgressive segregation for ear length (23 cm)

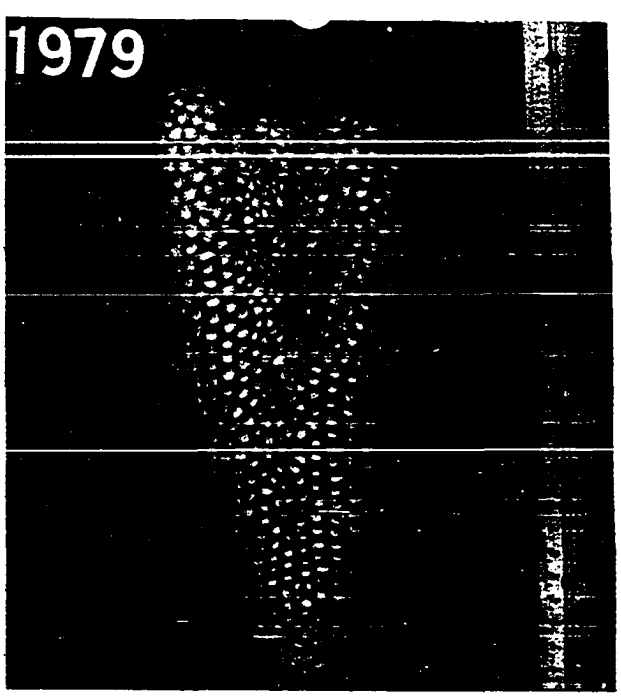
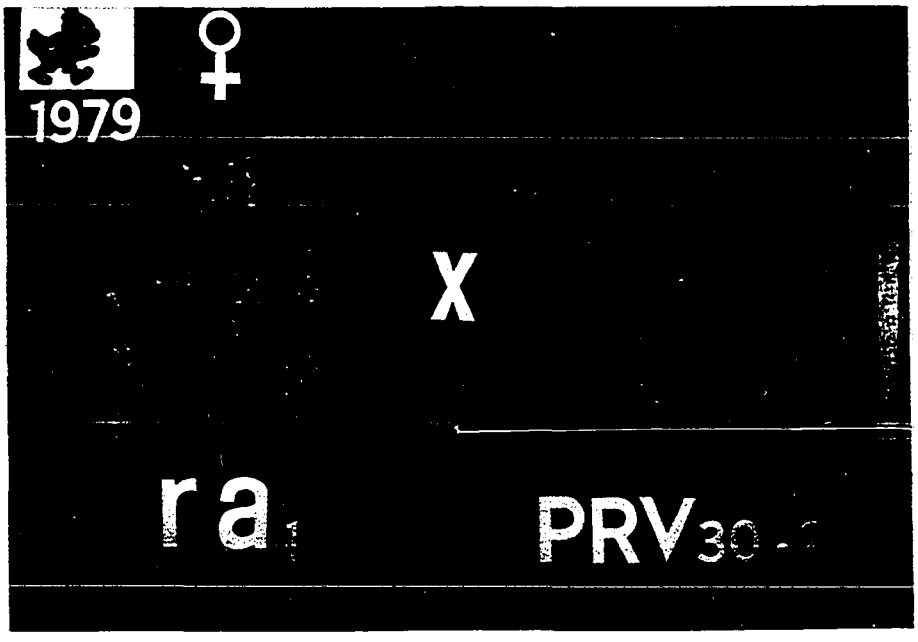

1979

Plate 16. Ears of the parents involved in the cross of a homozygous plant for ramosa 1 expression (ra1ra1) with PRV 30-25

Plate 17. S_1 progeny (S_2 seed) resulting from selfing the plant PRV 30-25 used as male parent in the cross with homozygous ramosa 1 source (ra1ra1) as shown in Plate 16


1979
♀
X
ra
PRV30

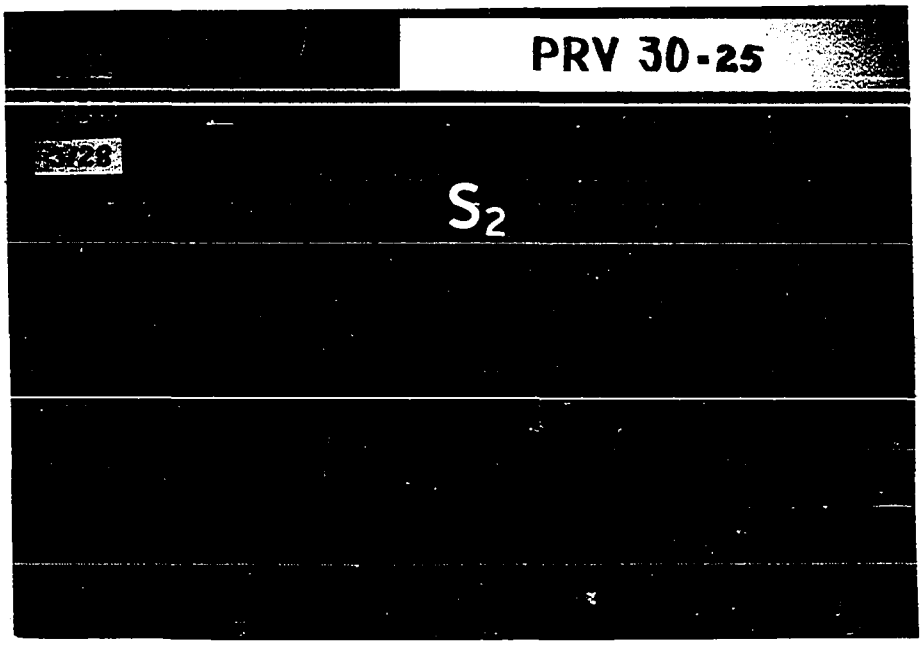
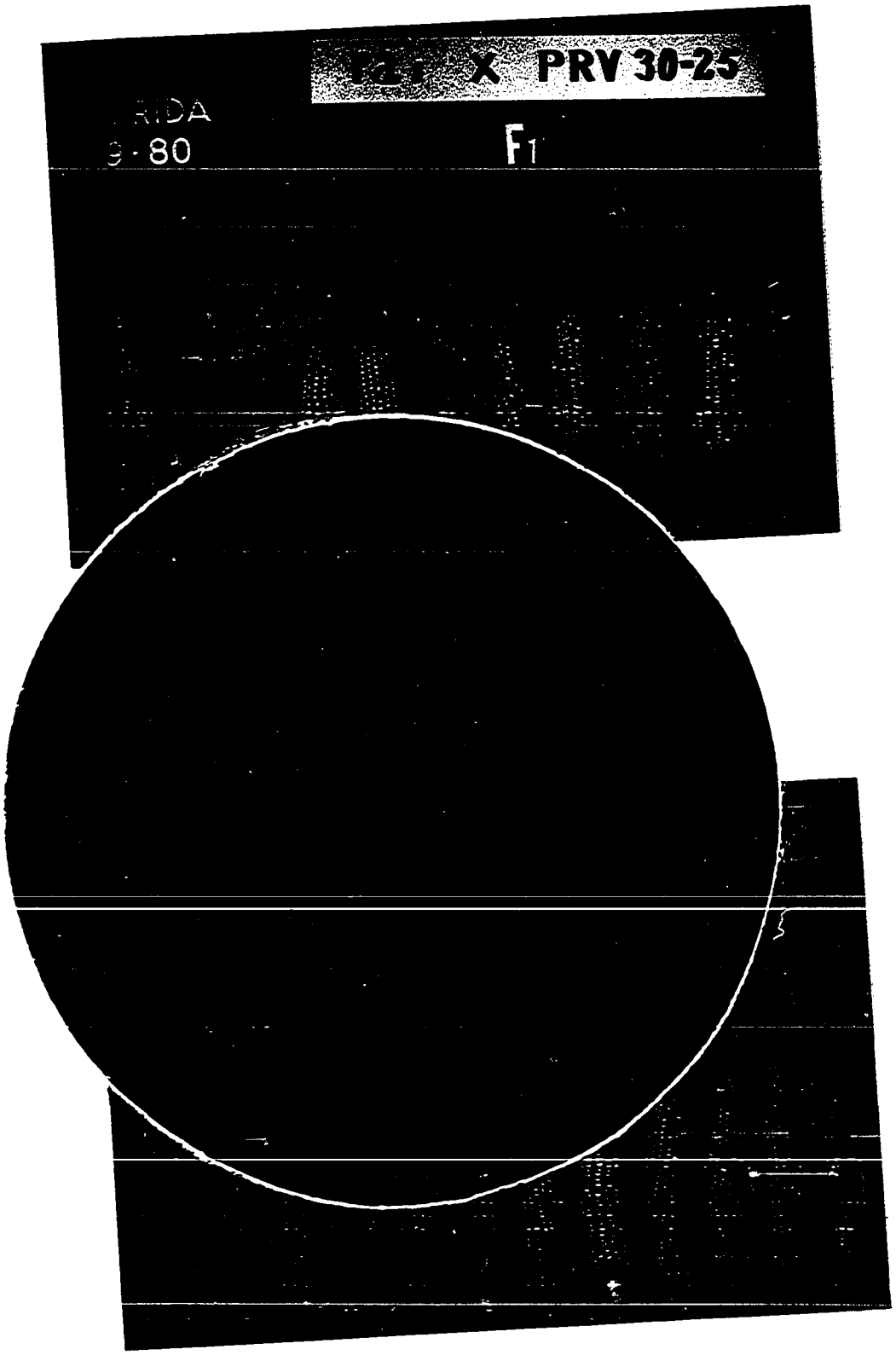
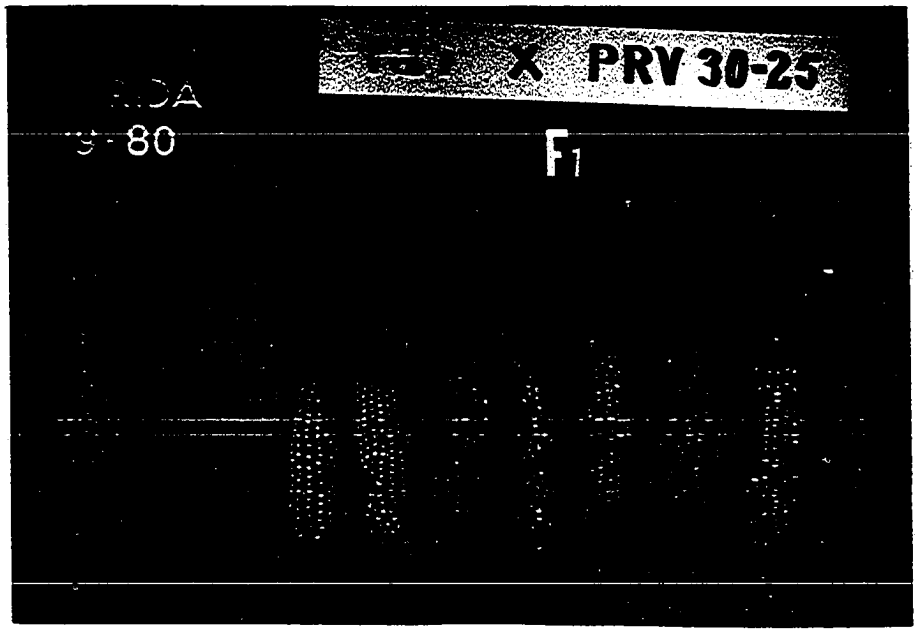

PRV 30-25
S2

Plate 18. F_1 generation from the cross between the homozygous source of ramosa 1 gene (*ra1ra1*) with PRV 30-25, as grown in Florida

Plate 19. F_1 generation from the cross between the homozygous source of ramosa 1 gene (*ra1ra1*) with PRV 30-25, as grown in Ames, Iowa


X PRV 30-25
F1


X PRV 30-25
F1

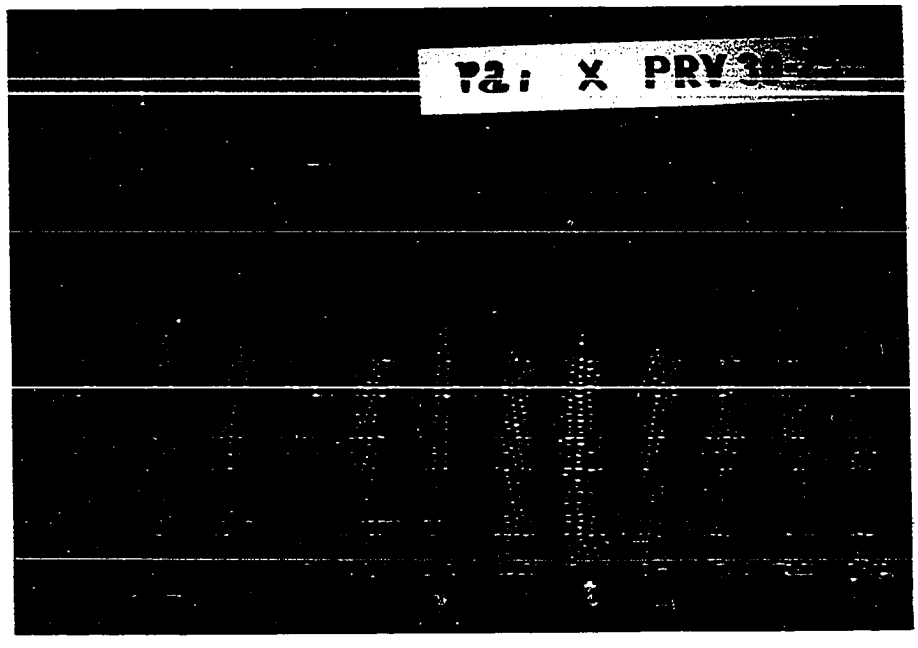
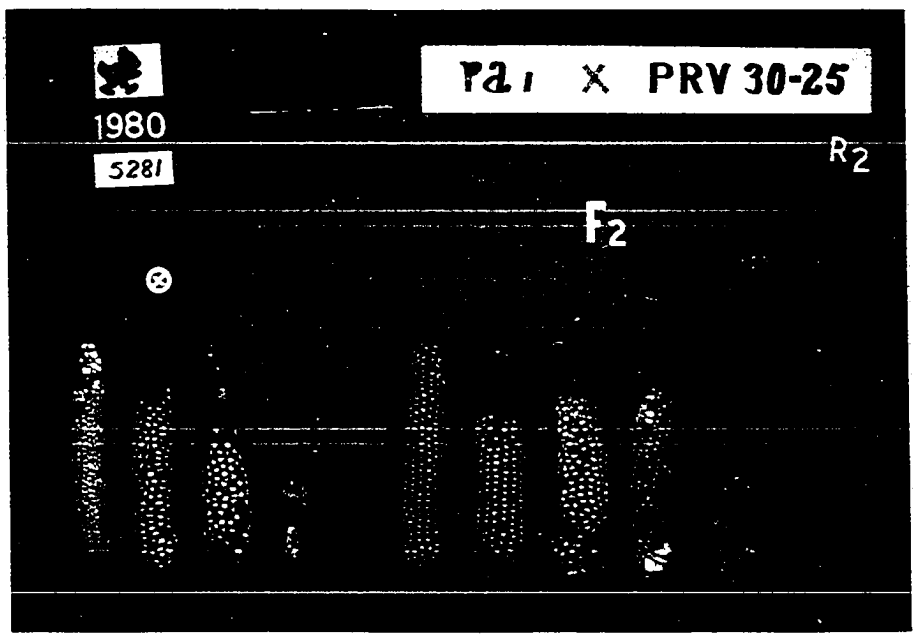


Plate 20. F_2 segregation from an F_1 ear rated 9 (incorrect notation shown on plate) for fasciation expression for the cross between the homozygous ramosa 1 source (ra1ra1) and PRV 30-25

Plate 21. F_2 segregation from an F_1 ear rated 9 (normal type) for fasciation expression for the cross between the homozygous ramosa 1 source (ra1ra1) and PRV 30-25


Pal × PRV 30-25
1980
5281
R2
F2

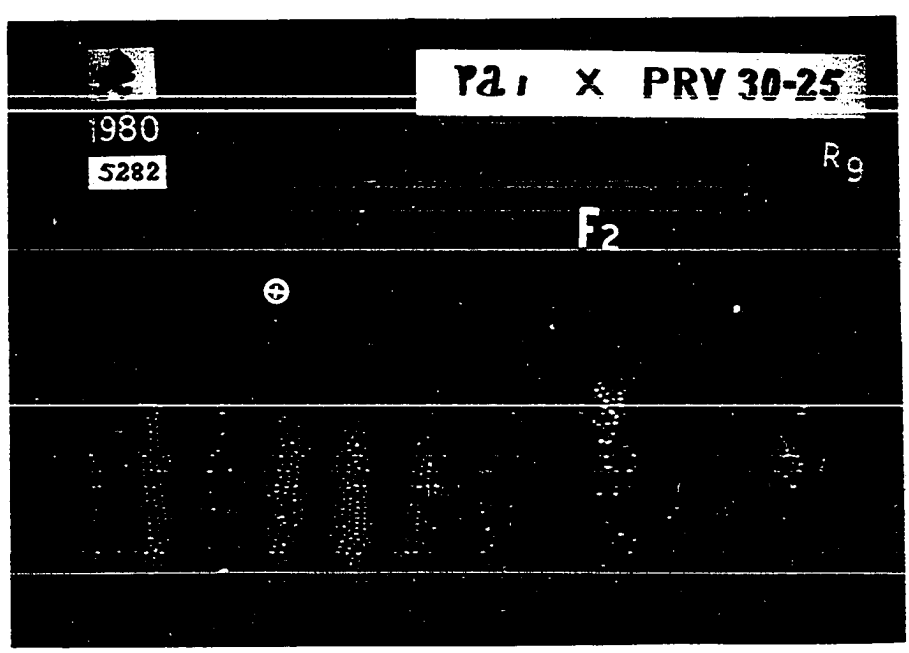
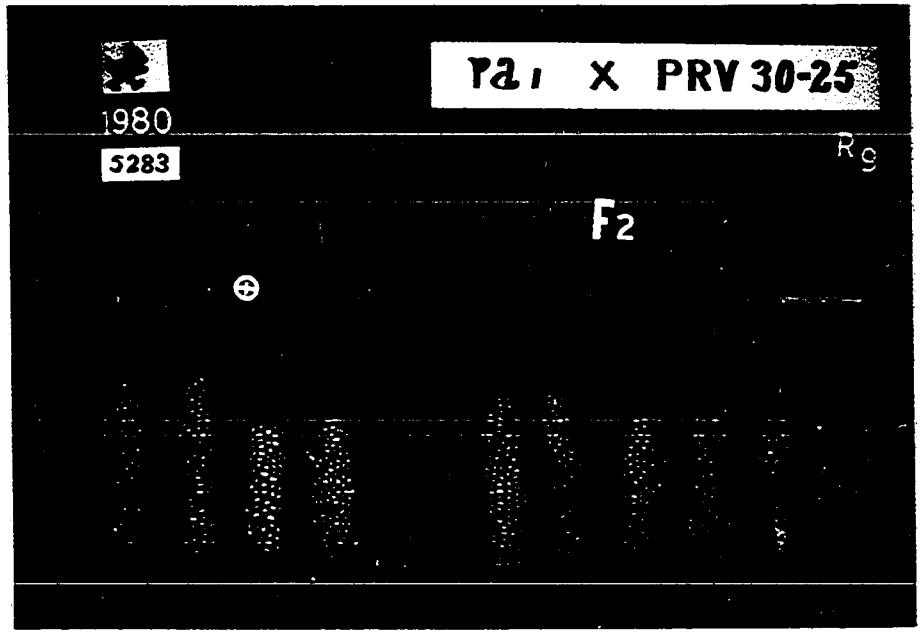

Pal × PRV 30-25
1980
5282
R9
F2

Plate 22. F_2 segregation from an F_1 ear rated 9 for fasciation expression for the cross between the homozygous ramosa 1 source (ralral) and PRV 30-25

Plate 23. Ears of the parents involved in the cross of a heterozygous plant for ramosa 3 expression (+ ra3) with PRV 30-56


1980
5283
ra1 X PRV 30-25
F2

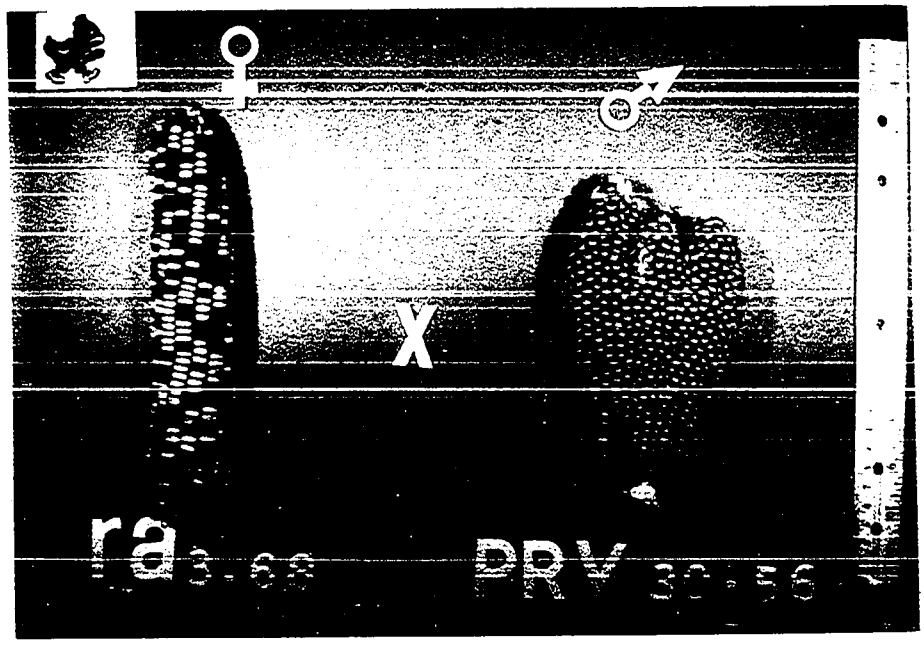
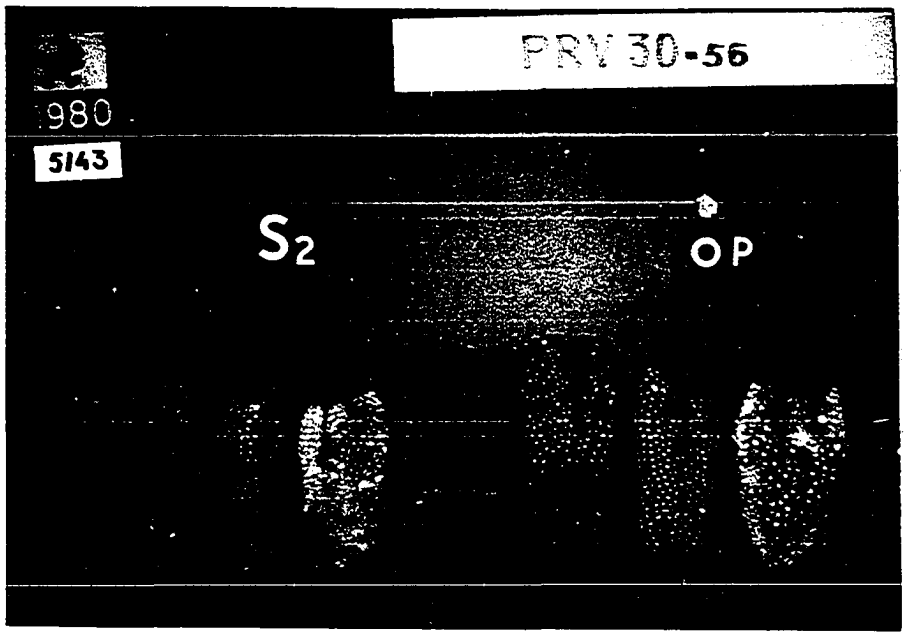
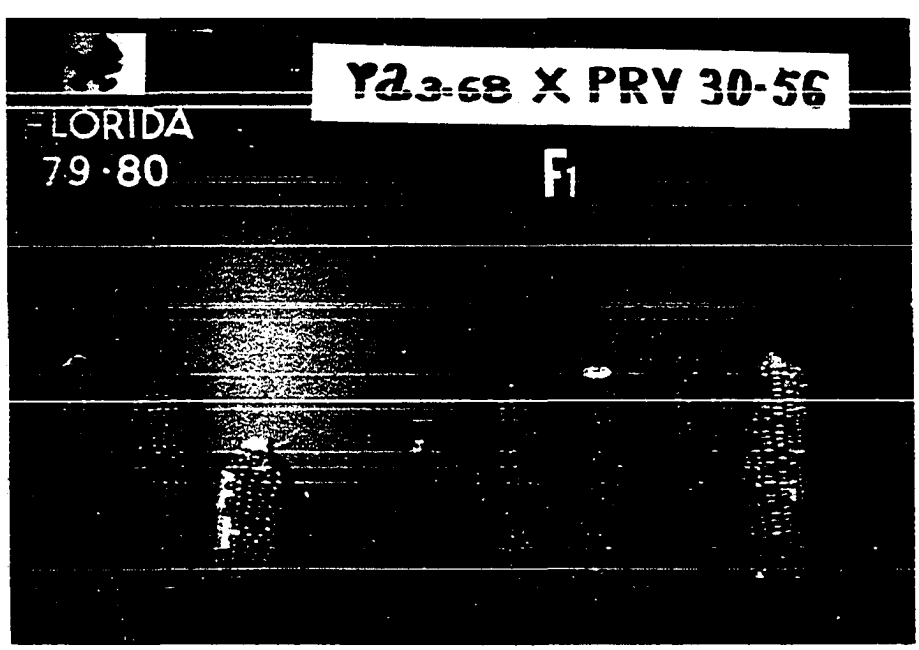

X
ra
PRV

Plate 24. S_1 progeny (S_2 seed) resulting from selfing the plant PRV 30-56 used as male in the cross with the heterozygous ramosa 3 source (+ ra3), as shown in Plate 23

Plate 25. F_1 generation from the cross between the heterozygous source of ramosa 3 gene (+ ra3) with PRV 30-56, as grown in Florida


PRV 30-56
980
5143
S2
OP


Ya3-68 X PRV 30-56
LORIDA
79-80
F1

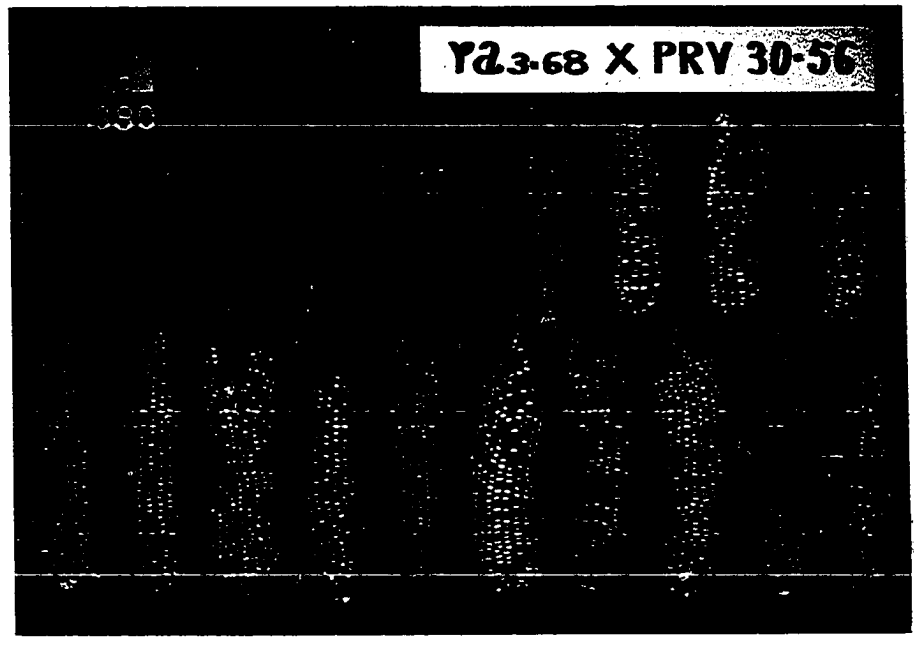
Subsequent generations were to be produced in the winter nursery in Florida in 1980-81.

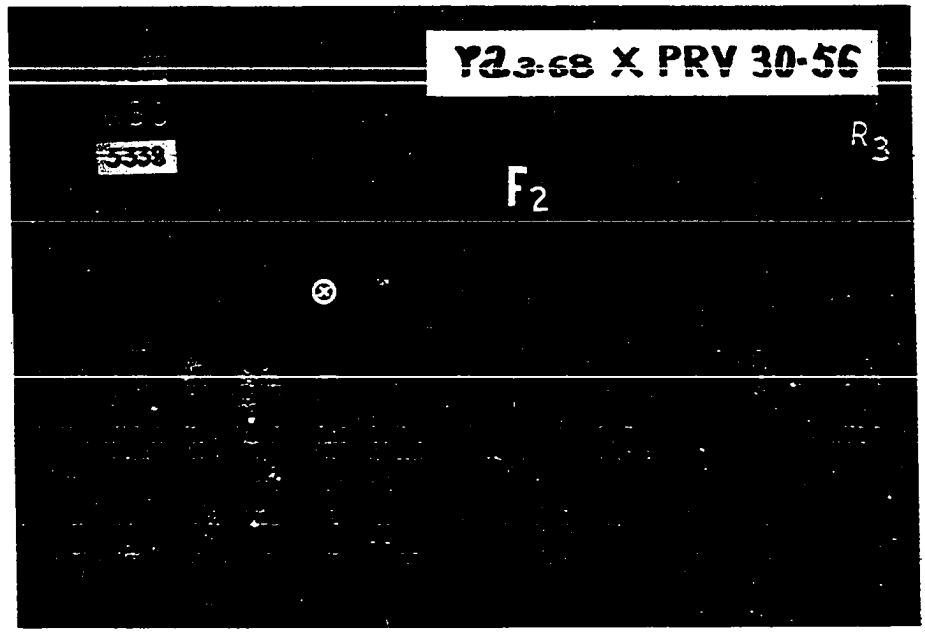
The following genetic material was grown in the nursery at Ames in the summer of 1980:

1. F_1 plants from the crosses between PRVs with ramosa sources ra1, ra2 and ra3 (Plates 19 and 26). We used remnant seed from that sent to Florida in 1979-80. These F_1s were grown and allowed to open pollinate with the double purpose of evaluating the ears for fasciation expression and making inferences about environmental effects by comparing the results with those obtained from the 1979-80 Florida winter nursery (Table A1).
2. S_0 plants from S_0 (F_2) seed produced in the 1979-80 Florida winter nursery. Because the large number of progenies was limiting our handling and processing capabilities, it was decided to pursue the studies only with the PRV that had the greatest expressivity of the fasciation character--PRV 30. S_0 plants of PRV 30 were selfed to obtain S_1 seed (Table A2).
3. S_1 plants from the selfed males in 1979 (Plates 17 and 24). These S_1s were selfed to obtain S_2 seed (Table A3).
4. A set of testcrosses with the inbred A632. These crosses were intended to constitute a test of

Plate 26. F_1 generation from the cross between the heterozygous source of ramosa 3 gene (+ ra3) with PRV 30-56, as grown in Ames, Iowa

Plate 27. F_2 segregation from an F_1 ear rated 3 for fasciation expression for the cross between the heterozygous ramosa 3 source (+ ra3) and PRV 30-56


Yd3-68 X PRV 30-56


Yd3-68 X PRV 30-56
R3
F2

dominance for the fasciation expression. A set of eight genotypes were testcrossed:

PRV 30-56
PRV 37-13
PRV 38-61
PRV 99-15
PRV 214-18
PRV 216-9
38-11/2-19
38-11/2-39

5. A diallel series of crosses among the following eight parents was produced:

PRV 30-56
PRV 37-13
PRV 38-61
PRV 99-15
PRV 214-18
PRV 216-9
38-11/2-19
WF9R

6. F_1s obtained in the greenhouse in the winter of 1979-80 were grown in the nursery for observation and selfing.
7. With the same objectives of studying problems related with allelism and dominance, we tried to make some crosses between PRV 30-56 with exotic germplasms, Zapalote and Chapalote Chico. However, these crosses were not successful.
8. Some seed of the double-cross hybrid HB 19 also was produced.

During the 1980 summer season, a visual classification for tassel expression was made in all genotypes grown. We

used a one digit rating from 1 (tassel with only the central branch) to 9 (ra1ra1 tassel, Plate 12). At harvest, all genotypes were classified for the fasciation expression. Also, photographs were taken for all ears of all genotypes involved to provide a photographic coverage. Since the beginning of our studies, we had a total of 938 slides of the ear expressions. These photographs, together with data collected, permitted us to follow the development of the different progenies and to study the respective segregations.

At this point of our research, we concluded that our studies based on the inheritance and segregation of a single major gene were not adequate. In fact, no evidence of allelism or dominance was found and the segregation in the crosses of the ramosa genes and presumed "ramosa" gene in the Portuguese varieties did not fit a model for single gene differences. The expressivity of the trait suggested several genes were involved, probably associated in complex genetic mechanisms, and that environmental effects would play an important role. Such a conclusion suggested that a quantitative genetics approach should be pursued to determine the expression of the abnormal ear shape. Based on the interpretations for the inheritance of the ear shape and the crosses and selfs made in 1980, replicated trials were planned to determine the fasciation expression in S_1 and S_2 progenies and crosses among lines. Emphasis was to be given

to the PRV 30 population to determine the quantitative basis of the abnormal ear shape.

Three groups of genetic materials were available for testing in field trials in 1981: (1) a set of 100 S_1 lines from the crosses of PRV 30 with ramosa sources ra1, ra2 and ra3; (2) a set of 90 S_2 lines from the selfed PRV 30 male plants; (3) a set of 50 entries that included eight parents, their 28 diallel single crosses (reciprocals not included), and 14 checks.

The S_1 progeny trials were conducted at two locations (Ames and Kanawha). The experimental field design was a randomized complete block design with 3 replications at each location. The experimental unit was a one-row plot hand-planted at 17 hills per row with hills spaced at 25.4 cm and a row width of 76.2 cm. The S_2 progeny trial was grown at Ames and the experimental technique was identical to that of S_1 progeny trials. The eight parents, their diallel crosses, and 14 checks were grown at Ames. The experimental design was a randomized complete block with 3 replications. The experimental unit included two rows spaced 76.2 cm and 5.1 m long. All plots were overplanted and thinned at the five-leaf stage to one plant per hill to give plant densities of approximately 56.600 plants/ha.

C. Measurements

The following set of 12 variables was measured or rated in all experiments conducted in 1981:

Variable	Description
FA	Fasciation expression: a visual rating with a range from 1 (phenotypic expression of an ear from a homozygous *ralral* plant) to 9 (a normal ear shape).
D_1-D_6	A set of six diameters measured in centimeters; D_1, D_3, and D_5 were measured, respectively, at the bottom, medium, and top of each ear when we face its largest diameters (Figure 2). D_2, D_4, and D_6 were measured, respectively, at the bottom, medium, and top of each ear when we face its smallest diameters (a 90^{o} turn along the length axis over the previous position, Figure 2).
R_1, R_2	Kernel row numbers; R_1 represents the number of kernel rows counted at the first third from the bottom of the ear. R_2 represents the number of kernel rows at the second third from the bottom of the ear (Figure 2).
L	Ear length: measured in centimeters from the base to the tip of the ear.

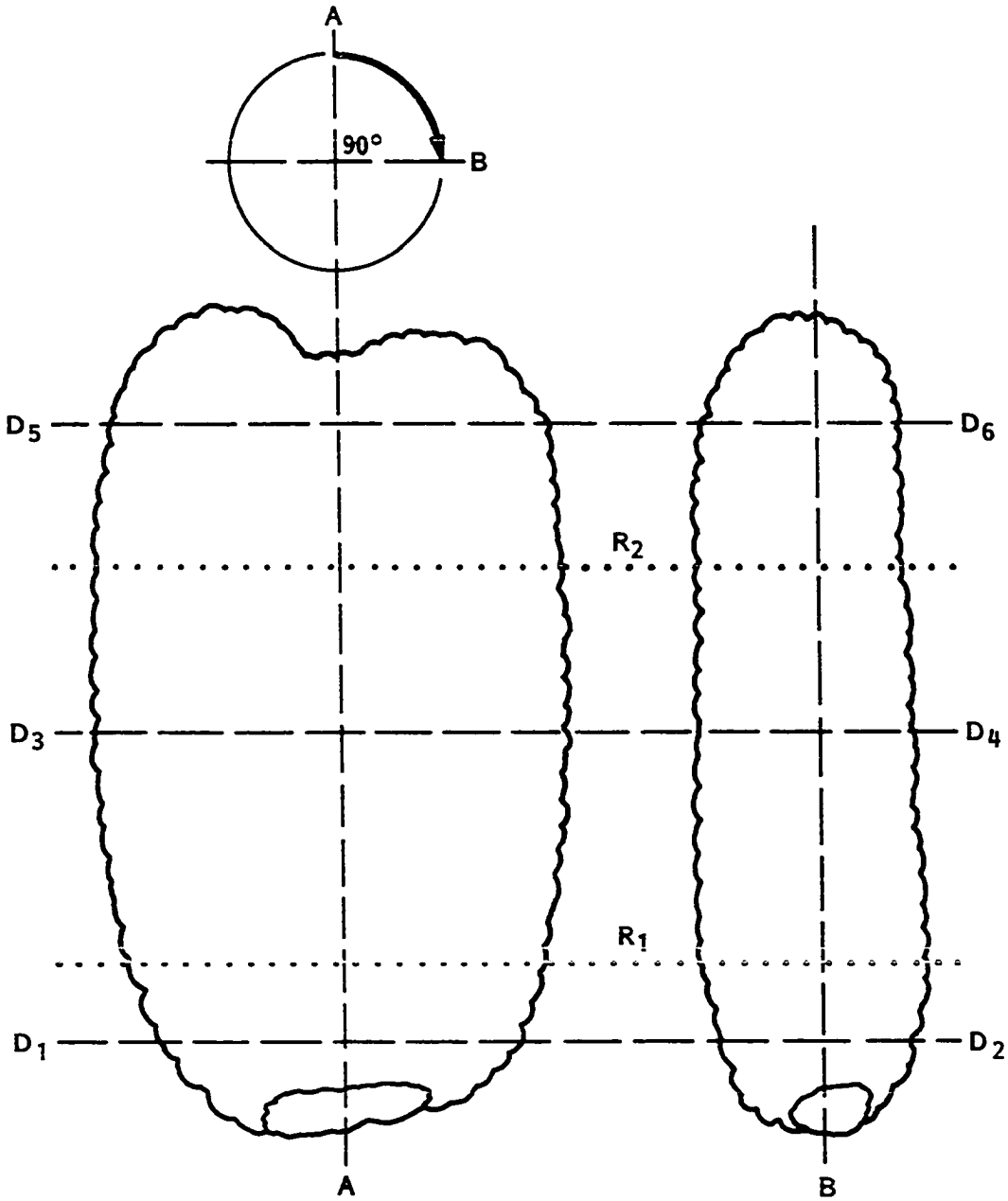


Figure 2. Two orthogonal views of the same ear showing the way the two sets of diameters and the two row numbers were measured and counted; in position A the diameters D_1, D_3 and D_5 were measured; in position B (a 90° turn along the length axis), D_2, D_4 and D_6 were measured

STD — Stand count: number of plants per plot counted after thinning and before harvest.

Y — Yield: the weight in grams of the dried (4% humidity) shelled kernels for each plot.

A summarization of the abbreviations and their descriptions for the traits is presented in Table 3.

D. Statistical Analysis

Approximately 200,000 measurements were taken for the three experiments (S_1s, S_2s and diallel). Based on the data collected from 1981 replicated trials, a statistical analysis was conducted for each trait in each experiment. A combined analysis for the two S_1 trials also was conducted.

1. Diallel

The standard statistical procedure for the diallel design was followed (Gardner and Eberhart, 1966). Because parents were considered fixed, our analysis was restricted to the calculations of genetic effects with special interest to general (GCA) and specific combining ability (SCA) effects. The source of variation, degrees of freedom, and expected mean squares are shown in Table 4.

Table 3. Listing of abbreviations used to describe the different traits for all the experiments

Abbreviations[a]	Description
FA	Fasciation expression (visual rating from 1 to 9)
D1	Diameter at the ear bottom, facing it at its biggest diameters (cm)
D3	Diameter at the ear medium, facing it at its biggest diameters (cm)
D5	Diameter at the ear top, facing it at its biggest diameters (cm)
D2	Diameter at the ear bottom, facing if at its smallest diameters (cm)
D4	Diameter at the ear medium, facing it at its smallest diameters (cm)
D6	Diameter at the ear top, facing it at its smallest diameters (cm)
R1	Number of kernel rows of the 1st third from the bottom
R2	Number of kernel rows of the 2nd third from the bottom
L	Ear length (cm)
STD	Stand count (number of plants/plot)
Y	Yield (g)

[a]Abbreviations will be used in all subsequent tables and text to describe the different traits.

Table 4. Source of variation, degrees of freedom, and expected mean squares for the analysis of effects for the diallel analysis of variance

Source	df[a]	MS	E(MS), Model I
Replications	r-1		
Entries	e-1	M_{18}	$\sigma^2 + rK_e^2$
Diallel	$[n(n+1)/2]-1$	M_{17}	$\sigma^2 + rK_D^2$
Parents	n-1	M_{16}	$\sigma^2 + rK_P^2$
Parents vs crosses	1	M_{15}	$\sigma^2 + rK_P^2$ vs X
Crosses	$[n(n-1)/2]-1$	M_{14}	$\sigma^2 + rK_X^2$
GCA	n-1	M_{13}	$\sigma^2 + [r(n-2)/(n-1)]K_{GCA}^2$
SCA	$n(n-3)/2$	M_{12}	$\sigma^2 + \{2r/[n(n-3)/2]\}K_{SCA}^2$
Diallel vs checks	1	M_{11}	$\sigma^2 + rK_D^2$ vs C

[a] r, e, n, c, t, and h indicate number of replications, entries, parents of diallel, checks, testcrosses, and hybrids, respectively.

Table 4. (Continued)

Source	df	MS	E(MS), Model I
Checks	c-1	M_{10}	$\sigma^2 + rK_C^2$
A632 testcrosses	t-1	M_9	$\sigma^2 + rK_A^2$
A632 testcrosses vs rest	1	M_8	$\sigma^2 + rK_{A \text{ vs } R}^2$
Rest	c-t-1	M_7	$\sigma^2 + rK_R^2$
Hybrids	h-1	M_6	$\sigma^2 + rK_H^2$
Portuguese hybrids	h-2	M_5	$\sigma^2 + rK_{PH}^2$
P. hyb. vs (A632xA619)	1	M_4	$\sigma^2 + rK_{PH \text{ vs } (A*A)}^2$
ra_1ra_1 testcrosses	c-t-h-1	M_3	$\sigma^2 + rK_{ra_1T}^2$
Hybrids vs ra_1ra_1 testcrosses	1	M_2	$\sigma^2 + rK_{H \text{ vs } T}^2$
Error	(r-1)(e-1)	M_1	σ^2
Total	er-1		

2. $\underline{S_1 s}$

The standard procedure (Steel and Torrie, 1960) for the randomized complete block design was used to analyze the data taken for different traits. Data were combined across the two environments and for the purpose of calculating the expected mean squares, environments, replications, and genotypes were assumed to be random. The sources of variation, degrees of freedom, and expected mean squares are shown in Table 5. Tests of significance were made according to the expected mean squares. Estimates of heritability on an entry mean basis were calculated from the combined analysis of variance by the following formula:

$$h^2 = \frac{\hat{\sigma}^2_G}{\frac{\hat{\sigma}^2}{re} + \frac{\hat{\sigma}^2_{GE}}{e} + \hat{\sigma}^2_G}$$

where:

h^2 = heritability estimate on S_1 progeny means;

$\hat{\sigma}^2_G$ = genotypic component of variance;

$\hat{\sigma}^2_{GE}$ = genotype x environment interaction component of variance;

$\hat{\sigma}^2$ = error component of variance;

e = number of environments; and

r = number of replications.

Phenotypic correlations were derived by the following formula (see Table 6):

Table 5. Source of variation, degrees of freedom, and expected mean squares for the combined analysis of variance for S_1 progeny trials

Source	df[a]	MS	E(MS)
Environments (E)	e-1	M_5	$\sigma^2 + g\sigma^2_{R/E} + r\sigma^2_{GE} + gr\sigma^2_E$
Reps/env	e(r-1)	M_4	$\sigma^2 + g\sigma^2_{R/E}$
S_1 progenies (G)	(g-1)	M_3	$\sigma^2 + r\sigma^2_{GE} + re\sigma^2_G$
G * E	(g-1)(e-1)	M_2	$\sigma^2 + r\sigma^2_{GE}$
Error	e(r-1)(g-1)	M_1	σ^2
Total	erg-1		

[a] e, r, and g indicate number of environments, replications, and S_1 progenies, respectively.

Table 6. Analysis of variance, covariance and expectations of mean cross products for a pair of traits (X and Y) over environments

Source	df[a]	Mean square X	Mean square Y	Mean cross product	Expected mean cross product
Environments	e-1				
Rep/env	e(r-1)				
Genotypes	g-1	M_{3_X}	M_{3_Y}	$M_{3_X}M_{3_Y}$	$\sigma_{XY} + r\sigma_{GE_{XY}} + re\sigma_{G_{XY}}$
G x E	(g-1)(e-1)	M_{2_X}	M_{2_Y}	$M_{2_X}M_{2_Y}$	$\sigma_{XY} + r\sigma_{GE_{XY}}$
Error	e(g-1)(e-1)	M_{1_X}	M_{1_Y}	$M_{1_X}M_{1_Y}$	σ_{XY}
Total	erg-1				

[a] e, r, and g indicate number of environments, replications, and genotypes, respectively.

$$r_{P_{XY}} = \frac{MCP_{3_{XY}}}{\sqrt{M_{3_X} \cdot M_{3_y}}} \quad ,$$

where:

$r_{P_{XY}}$ = phenotypic correlation coefficient for traits X and Y;

$MCP_{3_{XY}}$ = phenotypic mean cross product (covariance) for traits X and Y;

M_{3_X} = phenotypic mean square for trait X; and

M_{3_Y} = phenotypic mean square for trait Y.

Tests of significance were made using the following t-test (Steel and Torrie, 1960):

$$t = \frac{r}{\sqrt{1-r^2/n-2}}$$

where:

t = student's t statistic with n-2 df;

r = phenotypic correlation coefficient; and

n = number of paired observations.

Components of variance and covariance (Table 5 and Table 6) were used to estimate genotypic ($r_{g_{XY}}$) correlations (Mode and Robinson, 1959). The following formula was used:

$$r_{g_{XY}} = \frac{\hat{\sigma}_{G_{XY}}}{\sqrt{\hat{\sigma}^2_{G_X} \cdot \hat{\sigma}^2_{G_Y}}} \quad ,$$

where:

$r_{g_{XY}}$ = genotypic correlation coefficient for X and Y;

$\hat{\sigma}_{G_{XY}}$ = genotypic covariance between X and Y;

$\hat{\sigma}^2_{G_X}$ = genotypic variance of trait X; and

$\hat{\sigma}^2_{G_Y}$ = genotypic variance of trait Y.

A multiple regression analysis of all traits (FA, D_1, D_3, D_5, D_2, D_4, D_6, R_1, R_2, L, STD) upon yield (Y) also was conducted to evaluate the relative proportion of the contribution of the different possible models to the total yield sum of squares.

3. S_2s

The standard procedures (Steel and Torrie, 1960) for the randomized complete block design were used for the analysis of variance. Replications and genotypes were assumed random and the analysis of variance was conducted according to Table 7. An analysis of covariance, calculation of phenotypic and genotypic correlation coefficients, and calculation of the multiple regression analysis were conducted in a similar way to that for the S_1s trials conducted at one location.

Table 7. Source of variation, degrees of freedom, and expected mean squares for the analysis of variance for S_2 progeny trials

Source	df[a]	MS	E(MS)[b]
Replications	r-1	M_{12}	$\sigma^2 + e\sigma_R^2$
Entries	e-1	M_{11}	$\sigma^2 + r\epsilon^2$
S_2 progenies	g-1	M_{10}	$\sigma^2 + r\sigma_G^2$
S_2s vs checks	1	M_9	$\sigma^2 + rK^2_{G \text{ vs } C}$
Checks	c-1	M_8	$\sigma^2 + rK_C^2$
Ramosa sources	ra-1	M_7	$\sigma^2 + rK^2_{RA}$
Ramosa vs others	1	M_6	$\sigma^2 + rK^2_{RA \text{ vs } T}$
Others	t-1	M_5	$\sigma^2 + rK_T^2$
US inbreds	i-1	M_4	$\sigma^2 + rK_I^2$
Inbreds vs rest	1	M_3	$\sigma^2 + rK^2_{I \text{ vs } Z}$
Rest	z-1	M_2	$\sigma^2 + rK_Z^2$
Error	(r-1)(e-1)	M_1	σ^2
Total	re-1		

[a] r, e, g, c, ra, t, i, and z indicate, respectively, the number of replications, entries, S_2 progenies, checks, ramosa sources, others, US inbreds and rest.

[b] In the E(MS) for Entries, $\epsilon^2 = r[(n-1)\sigma_G^2 + K^2_{G \text{ vs } C} + (c-1)K_C^2]/e-1$.

IV. RESULTS AND DISCUSSION

A. Qualitative Genetics Approach

During the summer season of 1979 at Ames, 172 crosses were successfully produced by hand-pollination; these crosses included six PRV sources and one inbred (38-11/2), as shown in Table 8. During the 1979-80 winter season, the F_1 crosses were grown and selfed at the Florida winter nursery. Both the F_2 populations and S_1 progenies from the selfed male parents were grown at Ames in the summer of 1980. In addition to the genetic studies of the different progenies, an attempt was made to determine the relationship between the level of tassel branching and some characteristics of the ear.

1. Tassel studies

This study was focused on three progenies grown in 1980 at Ames: (1) the S_1 progenies from the selfed parents; (2) the F_2 populations from the F_1 crosses grown in Florida; and (3) the F_1 crosses produced in 1979 and grown at the 1979-80 Florida nursery were regrown at Ames in 1980 from remnant seed. Basically, these studies were oriented toward relating tassel shape (branching level) with two ear characters: fasciation intensity and kernel-row number in the ear. For level of tassel branching, a visual rating scale of 1 (tassel without secondary branches) to 9 (maximum of

Table 8. Number of successful hand-pollinated crosses realized in the summer of 1979 (Ames) between six PRV sources and one inbred line and ramosa genetic stocks

Male parent	Female parent				
	ra1ra1	+ ra1	+ ra2	+ ra3	Totals
PRV 30	1	5	7	16	29
PRV 37	0	10	2	6	18
PRV 38	1	4	9	10	23
PRV 99	0	6	7	18	31
PRV 185	0	4	6	6	16
PRV 214	1	0	4	8	13
PRV 216	1	2	5	10	18
38-11/2	1	1	11	10	24
Totals	5	32	51	84	172

branching, ra1ra1 type) was used. The F_1 tassels were rated on a plot mean basis, whereas the F_2 populations and S_1 progenies were rated on an individual plant basis. After harvest a visual classification for fasciation intensity for each ear and number of kernel rows per ear were made. The visual rating scale of 1 (ra1ra1 ear type) to 9 (normal type), described in Materials and Methods, was used.

Data for the F_1 crosses are presented in Table A4. Graphic presentations of these data are shown in Figures

3a and 3b, respectively, relating tassel shape with fasciation rating and kernel-row number. There was no significant relation between tassel branching and fasciation rating of the ear (b=0.11 and r=0.18; Figure 3a). No significant trend seemed to exist between tassel branching and kernel-row number (b=0.07 and r=0.14; Figure 3b).

Data for the F_2 generations are summarized in Appendix Table A2 and in Figures 4a and 4b. Figure 4a shows a negative trend (b=-0.16) between tassel shape and fasciation rating, with a negative correlation coefficient (r=-0.22) significant at 95% probability. But for tassel shape and kernel-row number, no significant relationship was found (b=0.05 and r=0.09; Figure 4b). Data from Figure 4a indicate that with greater branching of the tassels (higher values of tassel classification), we can expect a stronger fasciation expression (lower values of fasciation rating).

The S_1 progeny data are presented in Appendix Table A6 and plotted in Figures 5a and 5b. The S_1 progeny data show the same trend as was observed for the F_2 generations. The data for tassel branching, fasciation rating, and kernel-row number suggest two conclusions:

1. In PRV 30, tassel branching can be used as an indicator of the level of ear fasciation but not of kernel-row number both in the F_2s and S_1s. This is not in complete agreement with the findings of

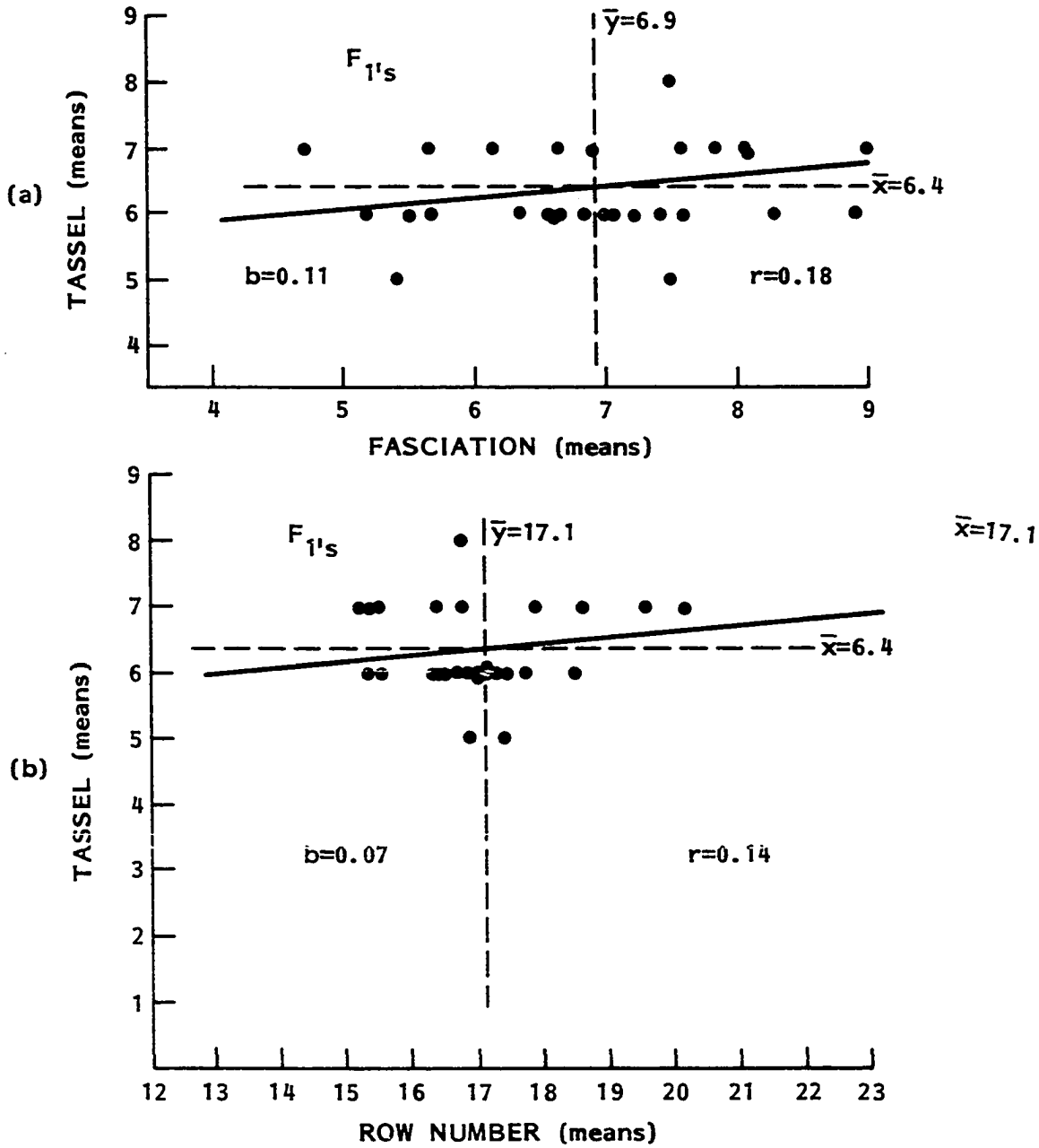


Figure 3. Relationship of tassel shape (level of branching) in the F_1 crosses with (a) fasciation intensity and (b) kernel-row number

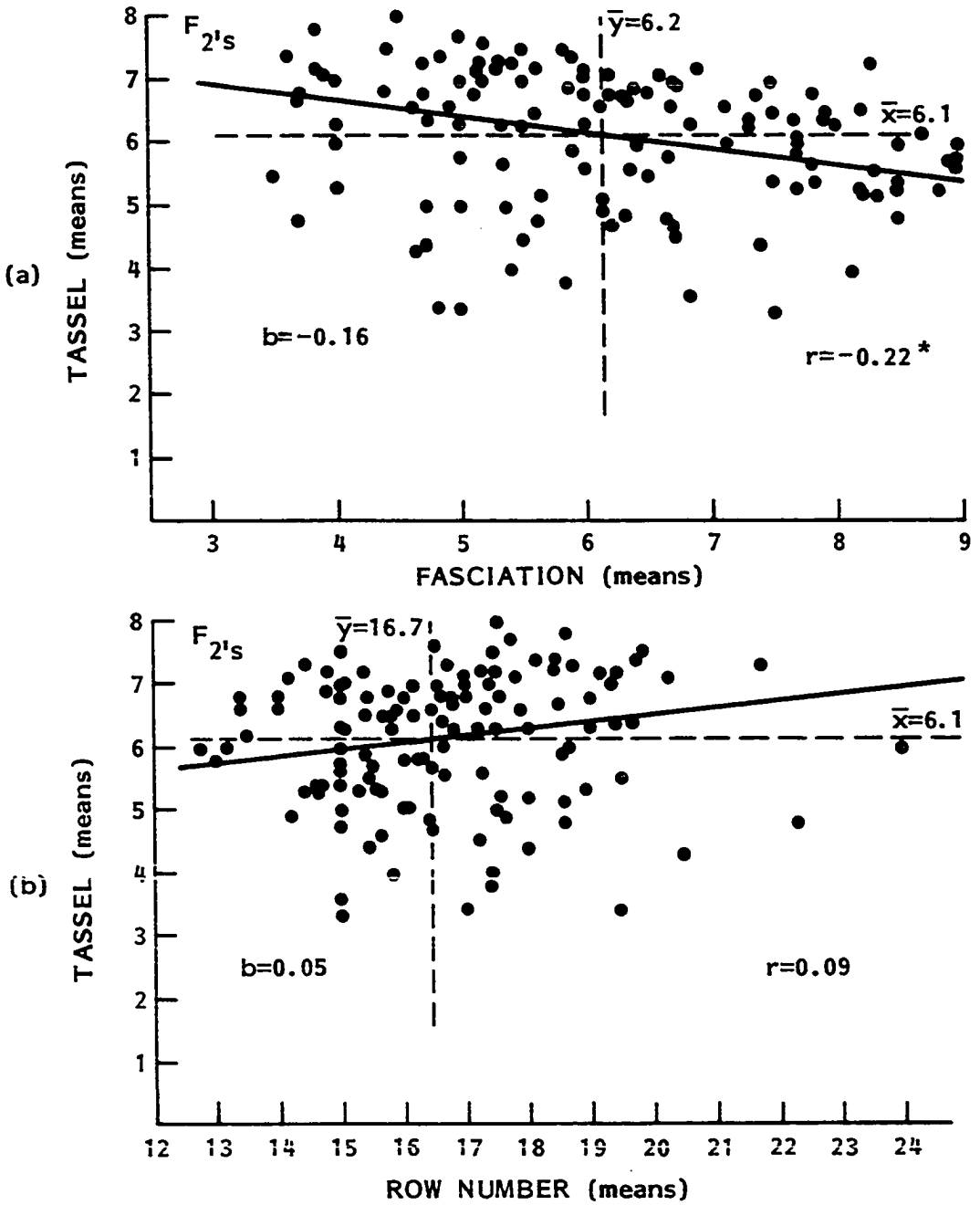


Figure 4. Relationship of tassel shape (level of branching) in F_2 populations with (a) fasciation intensity and (b) kernel-row number

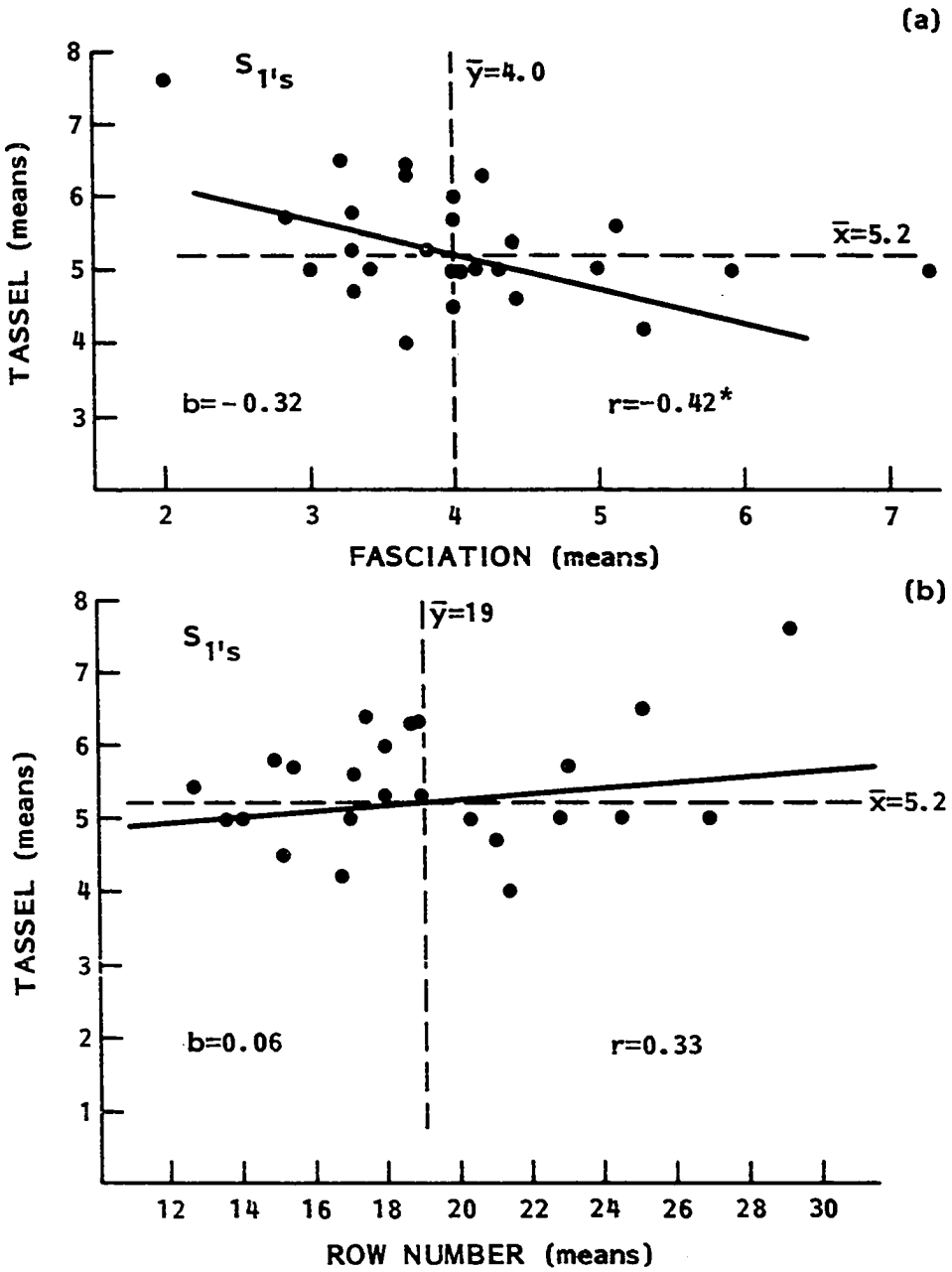


Figure 5. Relationship of tassel shape (level of branching) in the S_1 progenies with (a) fasciation intensity and (b) kernel-row number

Anderson (1944) for U.S. Corn Belt germplasm.

2. Because no definitive trends were shown in the F_1 crosses, this suggests that fasciation was expressed in the recessive condition.

2. Fasciation distribution

In attempting to study the distributions of the fasciated character in the different generations (F_1, F_2, and S_1), the data were grouped in three sets for the S_1 progenies and F_1 and F_2 generations, according to the three different ramosa genetic stocks (ra1, ra2, ra3). These three sets of crosses are listed in Table 9.

It should be emphasized that in my study we included genetic materials that were generally in the heterozygous condition and having considerable genetic variability. PRV 30 was an open-pollinated variety that would have genetic variation among plants, and also all three ramosa genetic stocks used in the crosses were in the heterozygous condition. An understanding of the degree and frequency of ear fasciation for the different progenies will be made for genetic materials that included genetic segregation.

Tables 10, 11, and 12 include the data of the three sets of crosses of PRV 30 with the genetic stocks ra1, ra2, and ra3 and the respective values of fasciation intensity for the F_1 and F_2 generations and the S_1 progenies. While I was primarily interested in studying the influence of each

Table 9. Crosses between PRV 30 and the three ramosa genetic stocks from which successful F_1 and F_2 generations were obtained

ra1ra1	ra1-	ra2-	ra3-
PRV 30-25	PRV 30-1	PRV 30-12	PRV 30-4
	PRV 30-3	PRV 30-19	PRV 30-5
	PRV 30-15	PRV 30-22	PRV 30-9
	PRV 30-17	PRV 30-34	PRV 30-23
	PRV 30-24	PRV 30-35	PRV 30-26
		PRV 30-36	PRV 30-29
		PRV 30-47	PRV 30-39
			PRV 30-41
			PRV 30-44
			PRV 30-45
			PRV 30-50
			PRV 30-53
			PRV 30-56
			PRV 30-57
			PRV 30-58

Table 10. Distribution of the F_1 and F_2 generations and S_1 progenies from the original crosses between different plants of PRV 30 and ral genetic stock, relative to their fasciation expression

Pedigree	Prog.[a]	Fasciation intensity (classes) 1	2	3	4	5	6	7	8	9
ralral x PRV 30-25	F_1	0	0	0	0	0	0	0	0	12
	S_1	-[b]	-	-	-	-	-	-	-	-
	F_2	6	0	1	1	4	7	0	4	9
+ ral x PRV 30-1	F_1	0	0	1	2	0	2	1	0	8
	S_1	-[b]	-	-	-	-	-	-	-	-
	F_2	0	0	5	3	6	5	4	2	4
+ ral x PRV 30-3	F_1	0	0	0	0	0	0	0	0	15
	S_1	0	0	4	5	0	0	0	0	0
	F_2	2	0	0	1	4	6	6	4	7
+ ral x PRV 30-15	F_1	0	0	1	0	1	0	0	0	8
	S_1	0	0	8	2	1	1	1	0	0
	F_2	2	1	1	2	6	5	3	6	9

[a] S_1 progenies are referred to the respective PRVs involved in the crosses.

[b] PRV 30-25 and PRV 30-1 were so affected by inbreeding depression that no measurements were taken in PRV 30-25 and no ears were obtained in PRV 30-1.

Table 10. (Continued)

Pedigree		Prog.	Fasciation intensity (classes 1	2	3	4	5	6	7	8	9
+ *ral* x PRV 30-17		F_1	0	0	0	0	0	0	1	1	9
		S_1	0	0	0	1	3	3	1	0	9
		F_2	0	0	0	0	0	2	4	5	4
+ *ral* x PRV 30-24		F_1	0	0	1	2	1	1	0	0	6
		S_1	0	2	2	1	0	0	0	0	0
		F_2	12	1	4	9	17	11	6	6	10
Totals	74	F_1	0	0	3	4	2	3	3	1	58
	44	S_1	0	2	14	9	4	4	2	0	9
	217	F_2	22	2	11	16	37	36	23	27	43

Table 11. Distribution of the F_1 and F_2 generations and S_1 progenies from the original crosses between different plants of PRV 30 and *ra2* genetic stock, relative to their fasciation expression

Pedigree	Prog.[a]	Fasciation intensity (classes)								
		1	2	3	4	5	6	7	8	9
+ *ra2* x PRV 30-12	F_1	0	0	0	0	3	1	1	2	9
	S_1	0	1	4	4	0	0	1	1	0
	F_2	0	0	0	8	10	7	4	6	9
+ *ra2* x PRV 30-19	F_1	0	0	0	1	2	2	1	3	5
	S_1	0	0	1	2	3	1	0	0	0
	F_2	0	0	1	3	12	5	5	0	4
+ *ra2* x PRV 30-22	F_1	0	1	2	1	5	1	0	2	3
	S_1	0	0	1	2	5	0	0	0	1
	F_2	0	2	1	6	3	3	3	2	13
+ *ra2* x PRV 30-34	F_1	0	0	0	1	3	2	4	1	4
	S_1	1	1	6	0	0	0	0	0	0
	F_2	10	1	5	14	25	15	6	10	7

[a]The S_1 progenies are referred to the respective PRV male parent.

Table 11. (Continued)

Pedigree		Prog.	Fasciation intensity (classes) 1	2	3	4	5	6	7	8	9
+ ra2 x PRV 30-35		F_1	0	0	0	1	0	0	3	3	8
		S_1	0	0	2	1	2	0	0	0	0
		F_2	0	1	0	2	3	8	5	5	2
+ ra2 x PRV 30-36		F_1	0	0	0	2	4	6	3	0	0
		S_1	0	0	2	2	1	0	0	0	0
		F_2	0	1	3	8	14	10	4	0	3
+ ra2 x PRV 30-47		F_1	0	0	0	0	2	1	1	5	5
		S_1	0	0	3	4	5	0	0	0	0
		F_2	0	0	0	12	17	4	3	2	8
Totals	104	F_1	0	1	2	6	19	13	13	16	34
	57	S_1	1	2	19	15	16	1	1	1	1
	305	F_2	10	5	10	53	74	52	30	25	46

Table 12. Distribution of the F_1 and F_2 generations and S_1 progenies from the original crosses between different plants of PRV 30 and ra3 genetic stock, relative to their fasciation expression

Pedigree	Prog.[a]	Fasciation intensity (classes) 1	2	3	4	5	6	7	8	9
+ ra3 x PRV 30-4[b]	F_1	0	0	0	0	3	4	5	3	1
	S_1^1	0	1	4	8	0	0	0	1	0
	F_2^1	0	1	1	4	3	0	1	2	12
+ ra3 x PRV 30-4[b]	F_1	0	0	0	0	2	0	0	3	10
	S_1^1	0	1	4	8	0	0	0	1	0
	F_2^1	0	0	0	1	2	3	3	9	8
+ ra3 x PRV 30-5	F_1	0	0	2	7	0	0	0	2	3
	S_1^1	0	1	4	2	0	0	0	0	0
	F_2^1	0	0	6	18	11	10	7	15	6
+ ra3 x PRV 30-9	F_1	0	0	2	3	0	0	1	1	6
	S_1^1	0	0	0	6	1	2	0	1	1
	F_2^1	0	0	1	5	2	3	4	7	19
+ ra3 x PRV 30-23	F_1	0	0	1	3	2	1	2	2	5
	S_1^1	0	0	3	10	0	0	0	0	0
	F_2^1	0	2	2	9	7	4	2	8	8

[a] The S_1 progenies are referred to respective male PRV.

[b] The same male parent PRV 30-4 was crossed to two different + ra3 female plants.

Table 12. (Continued)

Pedigree	Prog.	Fasciation intensity (classes) 1	2	3	4	5	6	7	8	9
+ ra3 x PRV 30-26	F_1	0	0	0	1	2	0	1	2	5
	S_1^1	0	1	2	3	0	0	0	0	0
	F_2^1	0	0	2	18	16	6	2	8	17
+ ra3 x PRV 30-29	F_1	0	1	0	3	2	0	0	1	9
	S_1^1	0	0	5	2	0	0	0	0	0
	F_2^1	0	1	1	4	2	7	2	7	13
+ ra3 x PRV 30-39	F_1	0	0	0	0	3	3	0	1	7
	S_1^1	0	0	0	7	1	0	0	1	0
	F_2^1	0	0	0	3	8	0	3	4	14
+ ra3 x PRV 30-41	F_1	0	0	1	6	3	1	1	1	1
	S_1^1	0	0	0	1	1	0	0	0	0
	F_2^1	0	0	3	12	6	6	7	13	33
+ ra3 x PRV 30-44	F_1	0	0	2	0	0	1	0	5	6
	S_1^1	0	0	0	0	0	1	0	0	0
	F_2^1	0	0	0	0	1	1	1	9	18
+ ra3 x PRV 30-45	F_1	0	0	0	1	2	2	2	3	3
	S_1^1	0	0	0	0	0	0	4	2	0
	F_2^1	0	1	1	5	0	0	2	1	10
+ ra3 x PRV 30-50	F_1	0	0	2	1	0	0	0	4	7
	S_1^1	0	0	4	3	1	0	0	0	0
	F_2^1	0	0	5	19	5	5	4	8	15

Table 12. (Continued)

Pedigree		Prog.	Fasciation intensity (classes) 1	2	3	4	5	6	7	8	9
+ ra3 x PRV 30-53		F_1	0	0	1	5	2	0	1	2	1
		S_1^1	0	0	2	6	0	0	0	0	0
		F_2^1	0	0	0	6	7	4	2	3	17
+ ra3 x PRV 30-56		F_1	0	0	7	1	2	0	2	1	1
		S_1^1	20	3	63	11	1	0	0	0	0
		F_2^1	2	5	11	16	6	6	7	3	5
+ ra3 x PRV 30-57		F_1	0	0	0	6	1	0	2	0	1
		S_1^1	0	0	1	2	0	0	0	0	0
		F_2^1	0	0	1	19	13	4	6	5	4
+ ra3 x PRV 30-58		F_1	0	0	0	2	0	2	3	4	4
		S_1^1	0	0	2	8	2	2	0	0	0
		F_2^1	0	0	2	5	5	5	6	6	23
Totals	211	F_1	0	1	18	39	24	14	20	35	70
	171	S_1^1	20	6	90	33	8	4	4	5	1
	739	F_2^1	2	10	36	144	94	64	59	108	222

ramosa genetic stock upon the PRV 30 in the F_1 and F_2 generations, the values of the S_1 progenies also are presented to facilitate making inferences about the genetic expression. Each group of genetic materials will be considered separately before making general conclusions.

a. F_1 generation The data included in Tables 10, 11, and 12 for the F_1 generations are represented graphically in Figures 6a, 6b, and 6c, respectively. Examination of the three F_1 generation distributions suggests the presence of different patterns of fasciation expression. The most distinct situation is represented in Figure 6a for the F_1s from the crosses between PRV 30 and the ra1 genetic stock. A very high percentage (78.4%) of normal type (9) ears strongly suggests recessiveness for the fasciation expression (Figure 6a). The distributions shown in Figures 6b and 6c, however, show a different type of pattern. The ra2 source (Figure 6b) seemed to moderately influence the F_1 distribution because there was a tendency to have two peaks. In Figure 6c, however, the proportion of fasciated to normal ears approximated a 1:1 ratio. Distributions of the crosses with ra1, ra2, and ra3 suggest patterns ranging from what seems to be a typical case of recessiveness (Figure 6a) to a 1:1 ratio (Figure 6c), which seems to suggest dominance in the heterozygous condition. Comparison of the F_1 vs S_1 values in Table 10 suggest the following genetic situations:

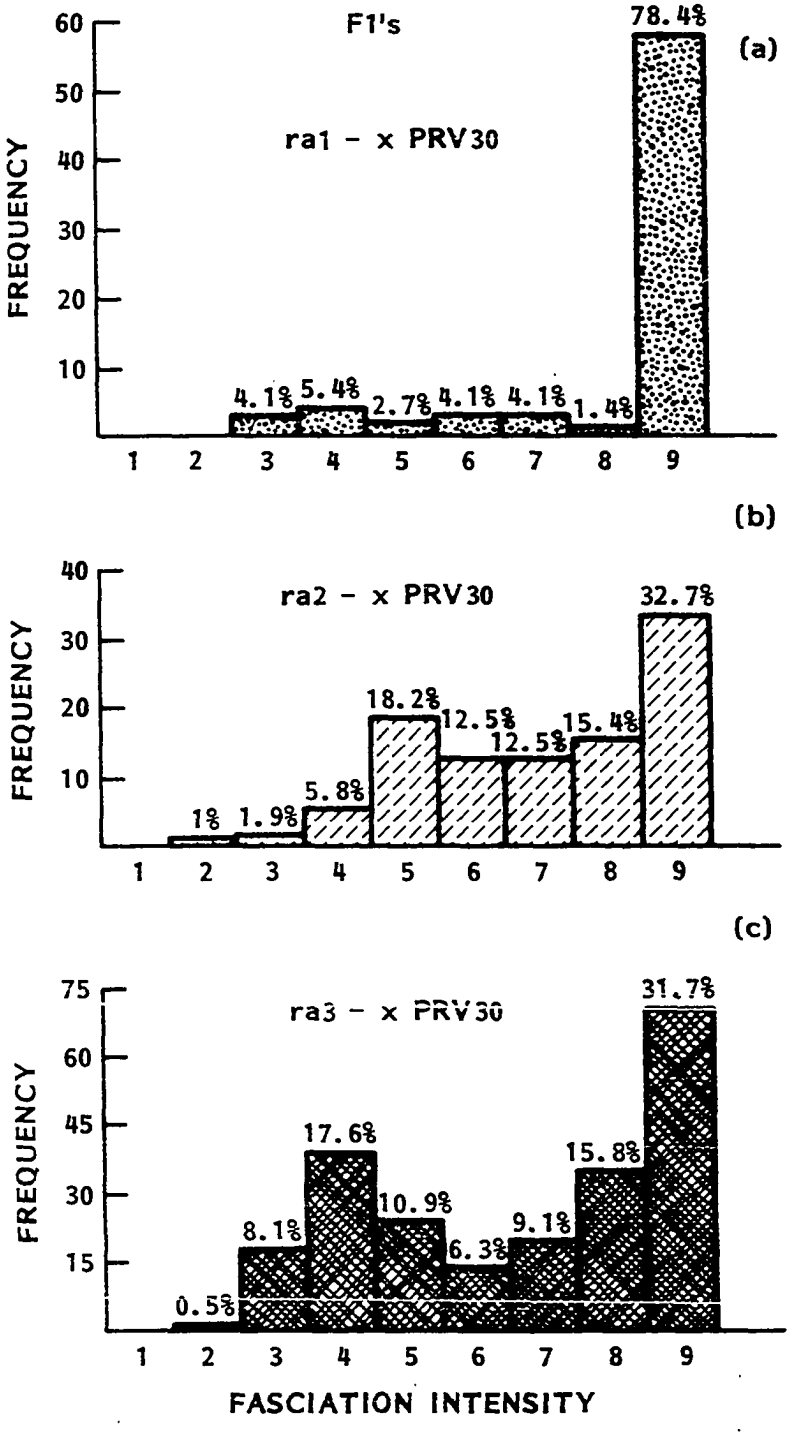


Figure 6. Fasciation expression in the F_1 crosses between PRV 30 and the ramosa genetic stocks for (a) ramosa 1 (ra1), (b) ramosa 2 (ra2), and (c) ramosa 3 (ra3)

1. F_1 generations of two plants--PRV 30-25 (Plates 18 and 19) and PRV 30-3--seemed to fit a model of recessiveness, with all ears of the normal type. S_1 progenies for PRV 30-3 also seemed to fit the same model of homozygous recessive.
2. PRV 30-24 F_1 was of the 1:1 type, suggesting a typical case of dominance in the heterozygous condition. However, when we consider the distribution of the S_1 progenies, we have to discard such a hypothesis because the S_1 progenies breed true for the fasciation expression.
3. Other crosses, for example PRV 30-15, suggest greater genetic complexities in the expression of fasciation.

Most of the crosses, however, seem to fit models of recessiveness, as illustrated in Figure 6a. The "two-peaks" pattern shown in Figures 6b and 6c suggest that among the F_1 crosses we have a few situations of some dominance in fasciation expression, which would be responsible for the first peak. The second peak could represent all the remaining F_1 crosses in which the recessiveness had an effect for the intensity of fasciation expression.

A question still remains, however, to explain the evident differences of the distributions shown in Figures 6a, 6b, and 6c. In other words, why did the F_1 crosses from the

genetic stock ra1 have a different pattern of expression as compared with those of ra2 and ra3. Some insight into this question may be possible by examining some possible combinations of genetic factors. Presence or absence of alleles for expression of fasciation may give different F_1 ratios if they were alone or in combination with a suppressor. For example, the following scheme shows:

fa fa (fasciated) x Fa Fa (normal)

↓

Fa fa - normal

or

fa fa U u (fasciated) x Fa Fa u u (normal)

↓

½ Fa fa u u - normal

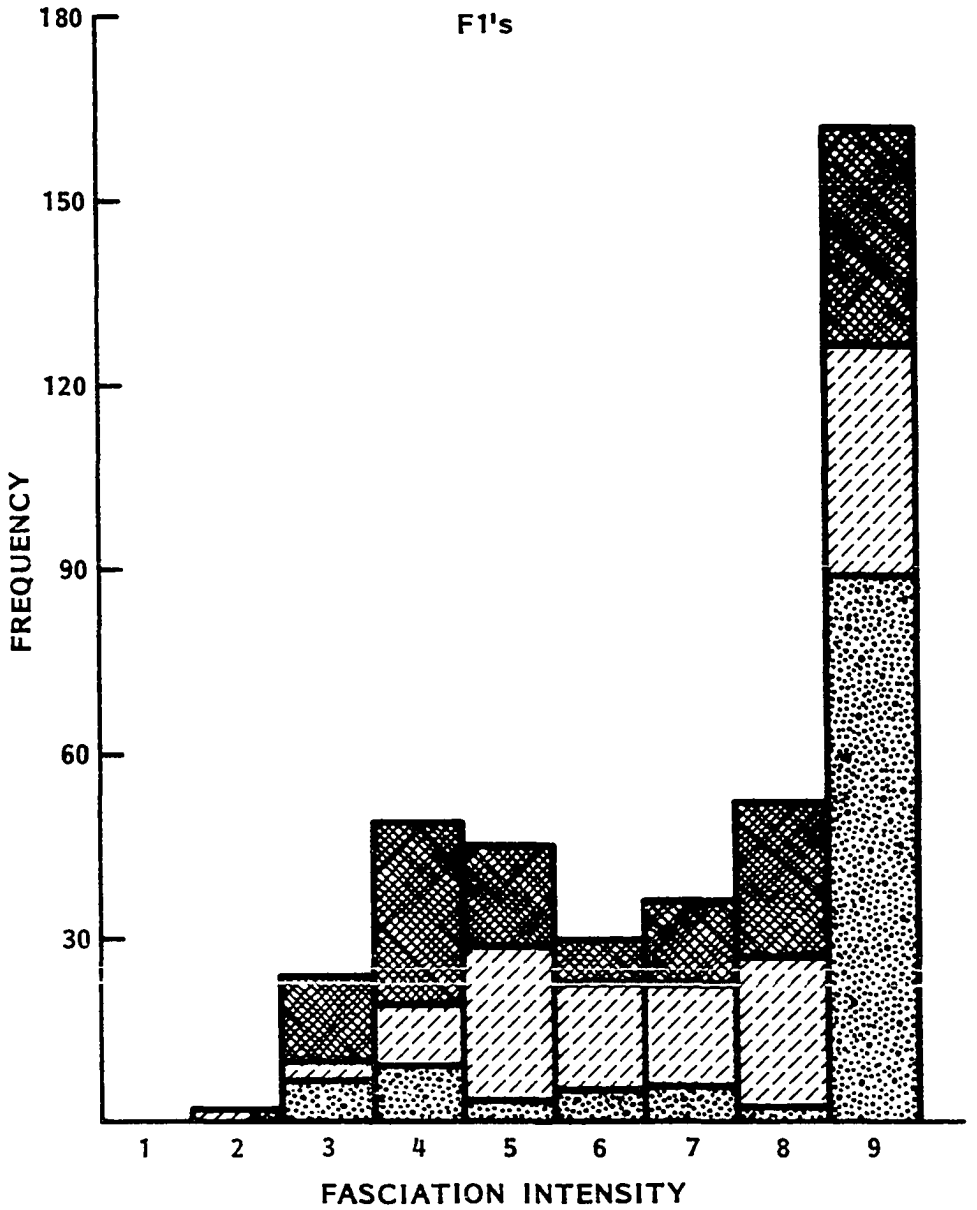
½ Fa fa U u - fasciated due to the presence of suppressor U acting on Fa

Another factor perhaps was because the same plants were not included in the three sets of crosses. PRV 30 was an open-pollinated variety and each plant included in the crosses would vary genetically one from another. The different genetic composition of the PRV 30 plants and also the heterozygosity of the ramosa stocks would contribute to the three different distributions for ra1, ra2, and ra3. We can also

speculate that part of the difference in expression of fasciation may be due to the differences in expression of ra1, ra2, and ra3 themselves (see Plate 14).

Another possibility to explain the differences among the distributions for intensity of fasciation would depend on the level of recessiveness; its expressivity in the F_1 may depend on the type of dominance (complete or partial) that the three ramosa sources exhibit. If this were the case, then ra1 source would possess a type of complete dominance for fasciation of the ear (Figure 6a). The ra2 and ra3 sources would have partial dominance, which, with the presence of suppressor genes (discussed later) could explain the occurrence of the two-peaks in Figures 6b and 6c.

Figure 7 is a summary of the data included in Figures 6a, 6b, and 6c. Figure 7 includes all of the F_1 crosses of PRV 30 with ra1, ra2, and ra3 and indicates the relative contributions of the different genetic stocks (ra1, ra2, ra3) to the different classes of fasciation expression. The cumulative data in Figure 7 show a two-peak situation similar to that for Figures 6b and 6c, and emphasize the strong contribution of genetic stock ra1 for the normal class (9). Data summarized in Figure 7 show a complete absence of the ramosa (ra1ra1) expression among all 389 F_1 crosses. This suggests an absence of allelism between ra1 genes and those of fasciation expression in the PRV 30 germplasm.



ra1-x PRV30	-	-	29.1	18.8	8.5	17.9	16.0	4.3	54.9
ra2-x PRV30	-	66.7	13.5	20.1	57.4	54.6	48.8	47.2	22.9
ra3-x PRV30	-	33.3	57.4	61.1	34.2	27.5	35.2	48.5	22.2

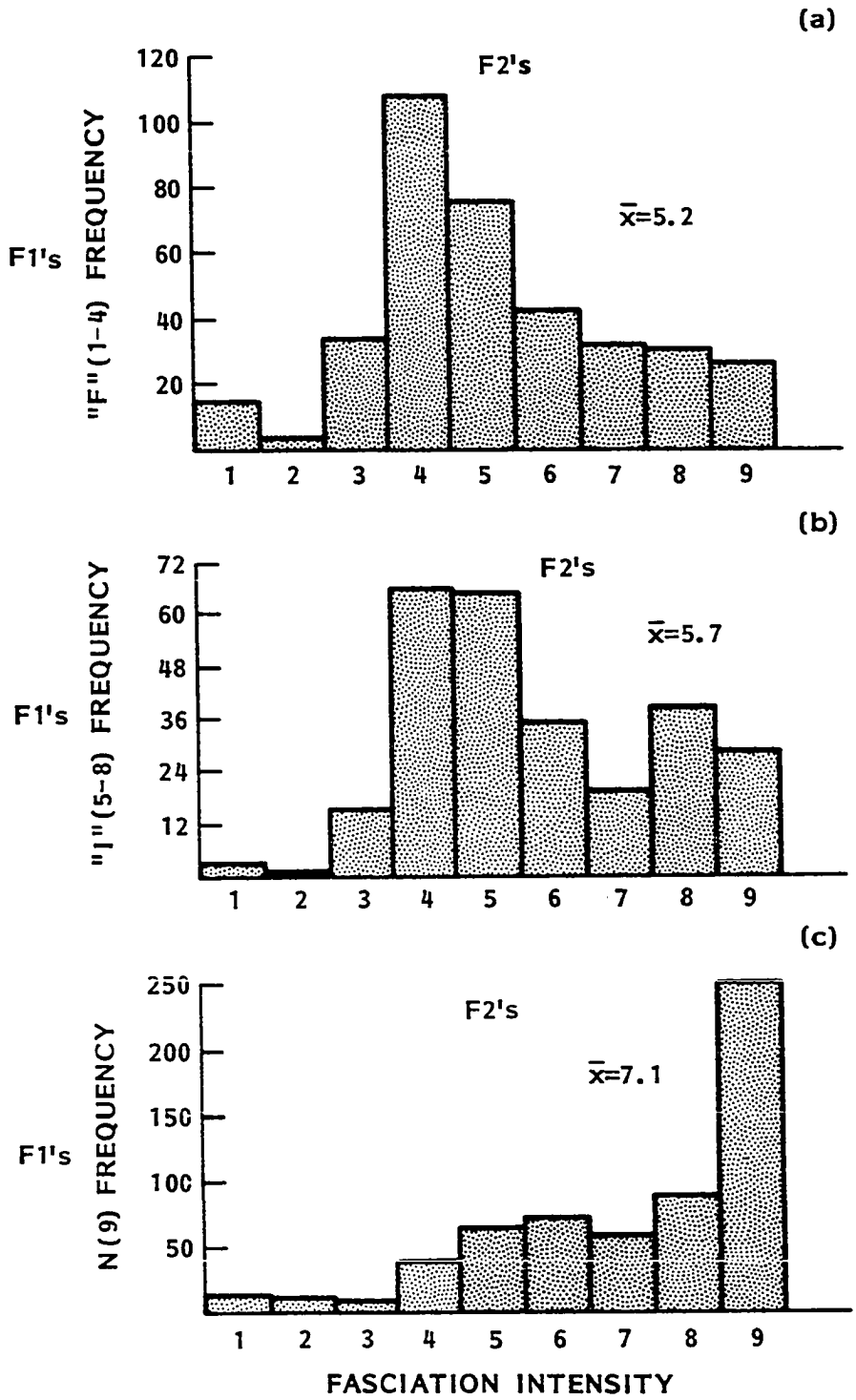
Figure 7. Summary of the fasciation expression in the F_1 crosses between PRV 30 and the three ramosa genetic stocks; percentage of contribution of each stock to each class of fasciation intensity is indicated

b. F_1 crosses vs F_2 generations Figures 8a, 8b, and 8c show the relation between the F_1 and F_2 generations for fasciation intensity of the ear. Figure 8a shows the distribution of the F_2 generations that originated from a set of highly fasciated (F) F_1 ears (ranked from 1 to 4). The F_2 distribution approaches a normal curve with a strong skewness to the left, suggesting partial dominance for fasciation expression. The highly fasciated material did not segregate in discrete classes, but tended to behave as a quantitative trait approaching a normal distribution in the F_2. Figure 8b includes the distribution of the F_2 generations generated from F_1 ears that had an intermediate expression (I) for fasciation (classified between 5 and 8). Figure 8b shows a two-peak situation, suggesting a preponderance of dominant gene action or more probably a situation involving suppressor genes, as discussed previously. Comparison of Figures 8a and 8b shows that the F_1 crosses that had a greater expression of ear fasciation (F) had a more complex genetic situation than those that had an intermediate (I) expression.

Figure 8c shows the expected trend for the F_2 progenies derived from a set of normal type (N) F_1 ears. There was a strong tendency for the F_1 ears classified as normal (N) to have a normal expression in the F_2 generation.

The means for the F_2 generations in Figure 8a ($\bar{x}$=5.2)

Figure 8. Relationship between the fasciation expression in F_1 crosses and their corresponding F_2 populations, where (a) F_2 distribution originated from fasciated (F) ears, (b) F_2 distribution originated from intermediate (I) ears, and (c) F_2 distribution originated from normal (N) ears


(a)
F2's
F1's
"F"(1-4) FREQUENCY
120
100
80
60
40
20
x̄=5.2
1 2 3 4 5 6 7 8 9
(b)
F2's
F1's
"I"(5-8) FREQUENCY
72
60
48
36
24
12
x̄=5.7
1 2 3 4 5 6 7 8 9
(c)
F2's
F1's
N(9) FREQUENCY
250
200
150
100
50
x̄=7.1
1 2 3 4 5 6 7 8 9
FASCIATION INTENSITY

and Figure 8b ($\bar{x}$=5.7) were very similar, whereas the means for the F_1 generations were very different (Figures 6a, 6b, and 6c). A more detailed relationship between the fasciation intensity values in the F_1 and F_2 generations is given in Figure 9. This suggests that it is possible to select the extreme types (strong fasciation and normal) in the F_1 generation, as shown in Figures 8a and 8c, and expect a similar expression in the F_2 generation. Figure 9 shows a fairly good relationship between the level of ear fasciation in the F_1 and F_2 generations. The linear trend suggested in Figure 9 indicates cumulative effects of duplicate genes, which would increase the fasciation expression in an additive manner.

c. F_2 generations Figures 10a, 10b, and 10c include the F_2 distributions for the crosses with each genetic ramosa stock. Because our data showed no allelism between ramosa and fasciation, we shall examine the F_2 distributions by isolating the left column (1) representing the ra1ra1 cases, from the other classes. We are most concerned with understanding and explaining the expressions of fasciation included in columns 2 to 9. Considering that Figures 10a, 10b, and 10c represent the F_2 generations for crosses between PRV 30 and the three ra1, ra2, and ra3 genetic stocks, respectively, a common pattern occurs in each distribution, suggesting two inferences: (1) each distribution tends to

FASCIATION EXPRESSION	
F1 vs	F2 (means)
1-2	5.3
3	4.8
4	5.4
5	5.8
6	5.5
7	4.6
8	5.8
9	7.1

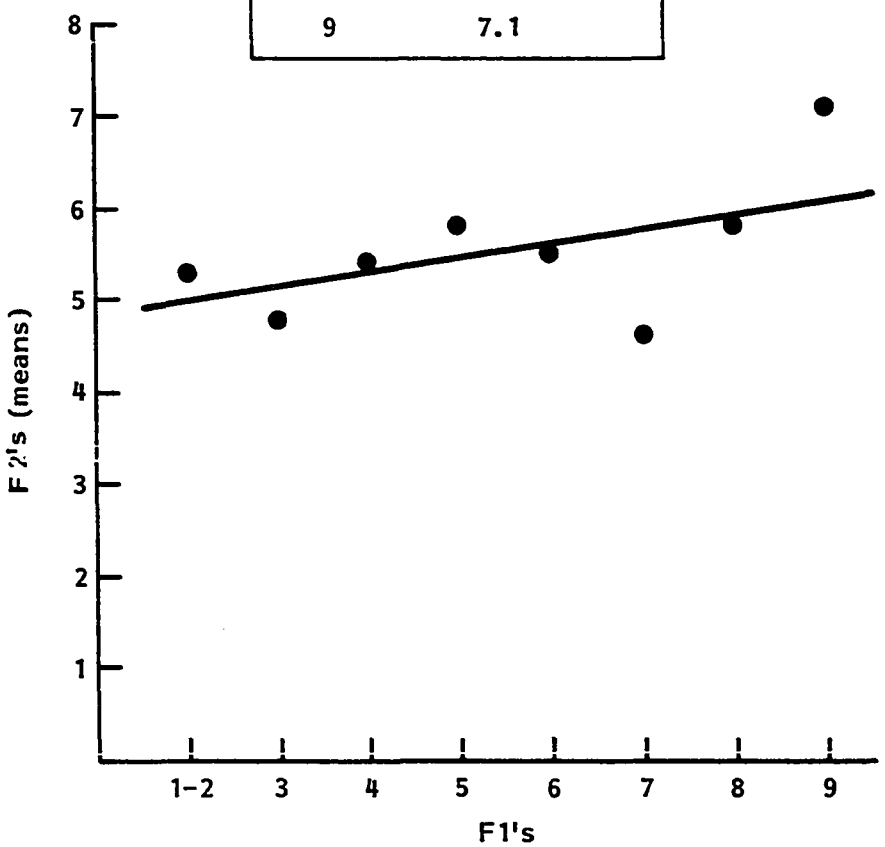
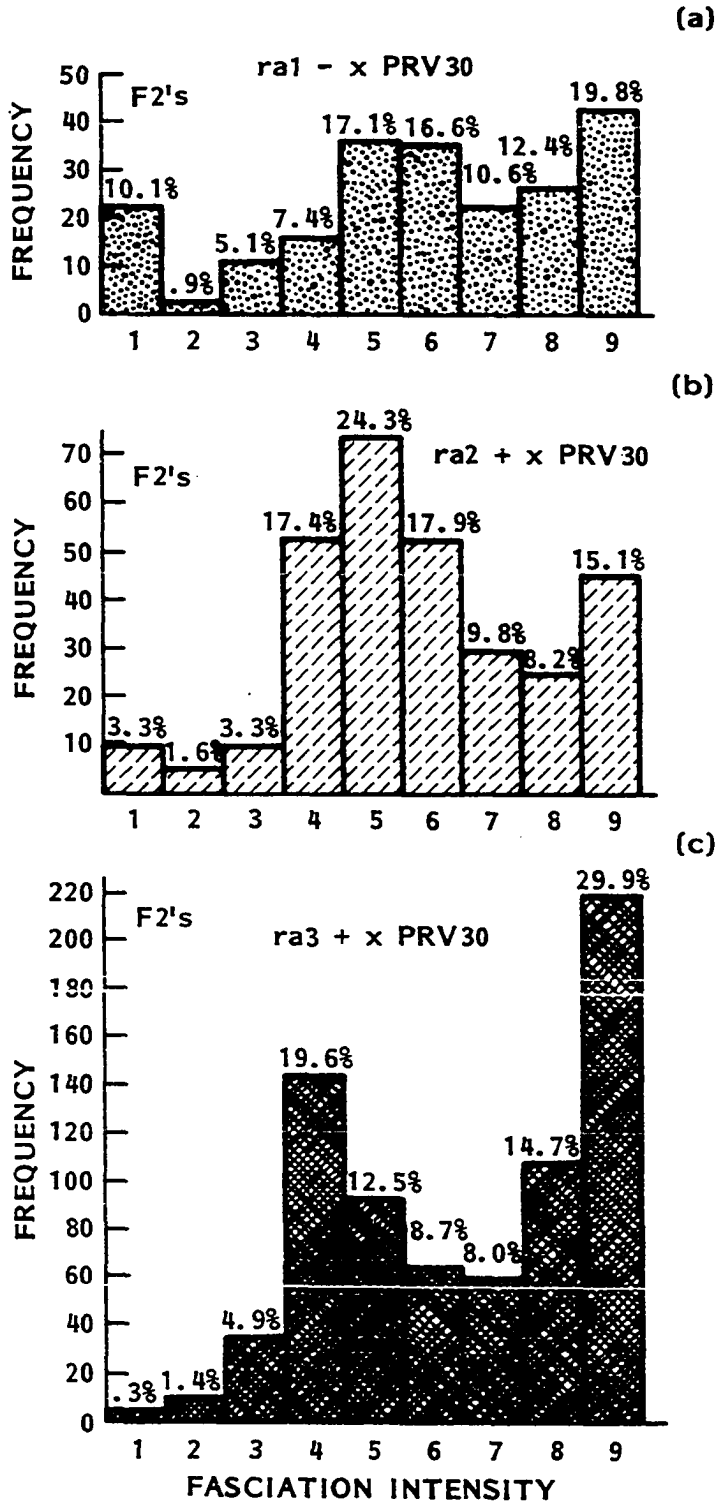


Figure 9. Relationship between fasciation expression in the F_1 crosses and their corresponding F_2 population

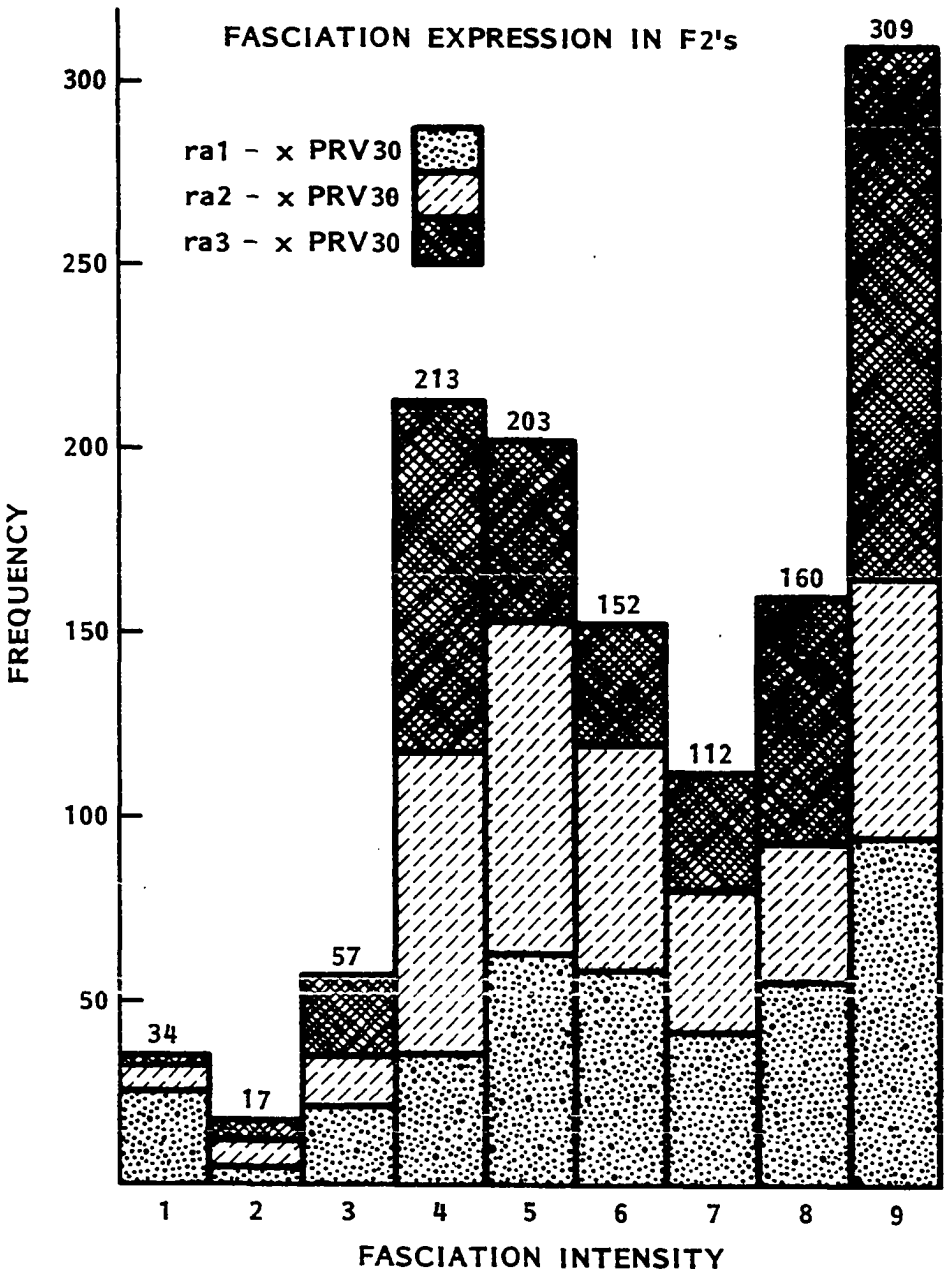
Figure 10. Fasciation expression in the F_2 populations between PRV 30 and their ramosa genetic stocks; (a) ramosa 1 (ra1), (b) ramosa 2 (ra2), and (c) ramosa 3 (ra3)


(a)
ra1 - x PRV30
F2's
FREQUENCY
50
40
30
20
10
0
10.1%
.9%
5.1%
7.4%
17.1%
16.6%
10.6%
12.4%
19.8%
1 2 3 4 5 6 7 8 9
(b)
ra2 + x PRV30
F2's
FREQUENCY
70
60
50
40
30
20
10
3.3%
1.6%
3.3%
17.4%
24.3%
17.9%
9.8%
8.2%
15.1%
1 2 3 4 5 6 7 8 9
(c)
ra3 + x PRV30
F2's
FREQUENCY
220
200
180
160
140
120
100
80
60
40
20
0
.3%
1.4%
4.9%
19.6%
12.5%
8.7%
8.0%
14.7%
29.9%
1 2 3 4 5 6 7 8 9
FASCIATION INTENSITY

have two-peaks, suggesting qualitative inheritance was involved, and (2) each distribution, however, does not fit the classical monohybrid, dihybrid, or trihybrid ratios.

Figure 11 summarizes the F_2 segregations included in Figures 10a, 10b, and 10c. Figure 11 shows the percentage contribution of each ramosa genetic stock to each of the nine classes of fasciation expression. The ra1 genetic stock had the greatest percentage of ears in class 1 (Figure 11). The remaining individuals in class 1 included very few from crosses with the other two sources (ra2, ra3). This suggests that PRV 30 also included the ra1 gene in its genetic background. Both ra2 and ra3 ramosa stocks did not include the ra1 gene and, consequently, ra2 and ra3 would not contribute individuals included in class 1. The two-peaks pattern was identical to that observed in Figures 10a, 10b, and 10c for the F_2 crosses. No simple genetic ratios occurred, which would support the use of some simple genetic model. Under these circumstances, it seems reasonable to assume that we probably have a genetic situation of a trait making a transition between a qualitative and a quantitative expression. It seems that the expression of the ramosa stocks was influenced by modifier genes and, perhaps, environmental factors at certain stages of development.

Figure 11. Fasciation expression (summary) in the F_2 generations from the crosses between PRV 30 and the three ramosa genetic stocks; percentage contribution of each stock to each class of fasciation intensity is indicated for crosses with each genetic stock



ra1 - x PRV30	73.7	23.1	38.4	16.7	31.7	38.4	37.3	35.1	30.6
ra2 - x PRV30	24.1	41.0	24.8	39.2	45.1	41.5	34.5	23.2	23.3
ra3 - x PRV30	2.2	35.9	36.8	44.1	23.2	20.1	28.2	41.7	46.1

3. Ramosa vs fasciation

An attempt was made, however, to understand some of the qualitative genetics involved in the ear expression, because some crosses did suggest that a simple genetic model would fit the data. Starting with some simple cases, we tried to sequentially develop models of increased complexity to gain some insight of what seemed to be some abnormal segregation ratios. For this approach, we used several sets of data, either of tassel classification before harvest or measurements and ratings of ears at harvest time. This phase of the genetic analysis was conducted first to explain the segregation ratios of the *ral* gene and, secondly, to explain the fasciation expression.

The set of data included in Table 13 served as the basis of analysis because of the diversity of situations in the F_2 generations from crosses between six PRV 30 plants and the ramosa stock *ral*. Given the previous conclusion of no allelism between the ramosa genes and fasciation, our attempted genetic models have to include the condition of no *ralral* plants in the F_1 generation. Given this common assumption for the six crosses included in Table 13, we also will have data obtained in each S_1 progeny.

One other comment should be made before initiating the study of each cross. It was shown previously that *ralral* plants were highly susceptible to corn smut (*Ustilago maydis*

Table 13. F_2 segregations for the ralral tassel expression for a set of six crosses between PRV 30 and the ramosa 1 (ral) genetic stock

Cross no.	Pedigree	Total no. plants	ralral tassel no.	Normal tassel no.	ralral/ total %
1	+ ral x PRV 30-24	109	20	89	18.3
2	+ ral x PRV 30-15	52	4	48	7.7
3	+ ral x PRV 30-3	33	2	31	6.1
4	+ ral x PRV 30-17	31	0	31	0.0
5	+ ral x PRV 30-1	35	0	35	0.0
6	ralral x PRV 30-25	41	14	27	34.1
Totals		301	40	261	13.3

L.), resulting in a high percentage of ear losses at harvest; the diseased ears reduced their contribution for the final number of ears included for classification. This means that the data obtained for tassel expression were more extensive than for the ear ratings. The distinction between the two tassel types was more easily determined, as shown in Plates 12 and 14.

From cross number 1 (+ ral x PRV 30-24), we obtained 109 F_2 plants that segregated for 89 normal type tassels and 20 ralral type tassel. In our approach to develop a simple genetic model, we also need to consider three

conditions: (1) in the F_1 crosses, all plants have to be normal; (2) in the S_1 progenies of PRV 30-24, no ramosa plants were obtained (Table 10); and (3) in the F_2 generation, we need a ratio that approximates a 1 ramosa to 4.5 normals. The simplest genetic model would be one of the type:

$$+ \underline{ral} \quad x \quad ++ \text{ (PRV 30-24)}$$

$$\downarrow$$

$$\tfrac{1}{2}(+ \underline{ral}) \quad F_1 \text{ - all normal}$$
$$\tfrac{1}{2}(++)$$

This model fits the first and second conditions, but fails to fit the third. The S_1 of PRV 30-24 (++) would breed true for the normal tassel and all the F_1 plants would have normal tassels. But, according to the model, the F_2 generation would segregate in a ratio of 7 normal to 1 ramosa, far from the observed proportion of 4.5 to 1. However, if we consider the hypothesis of the presence of a suppressor gene (Q) in PRV 30-24, we can obtain a closer fit to the observed values. Under this hypothesis, the genetic model should be of the following type:

$$+ \underline{ral}\ qq \quad x \quad \underline{ralral}\ QQ \text{ (PRV 30-24)}$$

$$\downarrow$$

$$\tfrac{1}{2}(+ \underline{ral}\ Qq) \qquad F_1 \text{ - all normal (N)}$$
$$\tfrac{1}{2}(\underline{ralral}\ Qq)$$

$$\downarrow$$

$$F_2 \quad \tfrac{1}{2}[1/16\ \underline{ralral}qq + 15/16N] + \tfrac{1}{2}[\tfrac{1}{4}\ \underline{ralral}qq + 3/4\ N]$$
$$\text{(ramosa)}$$

or

$$5/32\ \underline{ralral}qq + 27/32\ N$$
$$\text{(1 ramosa:5.4 N)}$$

$$[0.50 > P\ (X^2 \geq 0.627) > 0.25]$$

For the hypothesized genetic model, a significant X^2 value was not obtained. This genetic model approaches the observed segregation, but the power of the test was relatively poor. This hypothesized model has two important implications:

1. The *ral* gene was expressed only when there was no dominant suppressor gene; that is, it was expressed only when in the form *ralral*qq.
2. We would have to conclude that our PRV 30-24 possessed the *ral* gene in the homozygous condition. If this is true, such a conclusion would support our previous conclusion of an absence of allelism

between ral gene and fasciation genes.

From cross no. 2 (+ ral x PRV 30-15), we obtained 52 plants with a segregation of 4 ramosa to 48 normal tassels; that is, a ratio of 1 ramosa to 12 normals (Table 13). Following the previous hypothesis conditioning the ral expression to the genetic condition ralralqq, we obtained a model that fits exactly the observed values:

+ ralqq x ++ Qq (PRV 30-15)

↓

F_1

¼(++qq) N
¼(++Qq) N
¼(+ ralqq) N
¼(+ ralQq) N

↓

F_2

5/64 ralralqq + 59/64 N
(1 ramosa:12 N)

With this model, we satisfied all the conditions. The S_1 generation will be all normal (see Table 10); the F_1 cross also will be all normal; and the F_2 segregation fits the hypothesized model. Hence, according to our model, PRV 30-15 possessed the suppressor gene Q, but not the ral gene. Also, this model would substantiate our model for cross no. 1.

For cross no. 3 (+ ral x PRV 30-3) in Table 13, we obtained 33 plants with a segregation of 2 ramosa to 31 normal tassels. In cross no. 3, we considered it reasonable

to assume a situation identical to cross no. 2, and the same genetic model would be applicable. The X^2 test, with the same limitations already mentioned, was not significant ($X^2 = 0.366$) for cross no. 3.

From cross no. 4 (+ ral x PRV 30-17), we had 31 plants with normal tassels for all plants. Although only 31 plants were available to classify for tassel expression, the following genetic model is suggested, based on the previous conditions:

$$+\ \underline{ral}gg \quad x \quad ++QQ \text{ (PRV 30-17)}$$

$$\downarrow$$

$$\tfrac{1}{2}(++\underline{Q}g) \qquad N$$

F_1 $\qquad\qquad \tfrac{1}{2}(+\ \underline{ral}\ \underline{Q}g) \qquad N$

$$\downarrow$$

$F_2 \qquad 1/32\ \underline{ral}\underline{ral}gg + 31/32 \quad N$

(1 ramosa:31 N)

$$[0.50 > P(X^2 \geq 1.033) > 0.25]$$

According to this model, PRV 30-17 did not contain the ral gene, and all the conditions for the S_1 and F_1 (see Table 10) generations would be met.

Cross no. 5 (+ ral x PRV 30-1) included 35 plants and all plants had normal tassels (Table 13). This cross was similar to cross no. 4, and we assumed the same genetic model. For cross no. 5, we also have a nonsignificant X^2 test ($X^2 = 1.029$).

Cross no. 6 (ralral x PRV 30-25) (Plate 16) included 41 plants that had a segregation ratio of 14 ramosa to 27 normal tassels in the F_2 generation (Table 13; for ear segregation see Plates 20, 21, and 22). The F_2 segregation in cross no. 6 approximates a 1:2 ratio. The F_1 plants had all normal tassels (Table 10; for ear expression see Plates 18 and 19) and the S_1 progenies gave no evidence of any ralral ears (Plate 17). The results for cross no. 6 were unexpected because it was one of the few cases where the female parent was homozygous for the ramosa expression (ralral) (Plate 16). All attempts to fit a simple and reasonable genetic model to describe the unexpected 1:2 ratio obtained in the F_2 generation failed. This seems to be an example that requires a more complex genetic model, probably assuming the presence of one or more modifiers or regulatory genes and a polyhybrid genic situation.

Another set of data was obtained from F_1 crosses produced from a set of crosses in the greenhouse during the winter of 1979/80 at Ames. This set of crosses was produced to substitute for some of the crosses that failed in the field in 1979 due to the high susceptibility of the homozygous ramosa plants to corn smut. In the greenhouse, we used the homozygous plants (ralral) as males in the crosses with PRV 30 and two inbreds. The data from the F_1s and the respective pedigrees of each cross are given in Table 14.

Table 14. ra1ra1 tassel expression in a set of seven crosses (F_1) between five PRVs and two inbreds and the ramosa 1 (ra1ra1) genetic stock

Cross no.	Pedigree	Total no. plants	ra1ra1 tassel no.	Normal tassel no.
7	PRV 30-71 x ra1ra1	47	12	35
8	PRV 37-17 x ra1ra1	63	0	63
9	PRV 38-88 x ra1ra1	75	0	75
10	PRV 99-89 x ra1ra1	30	0	30
11	PRV 216-101 x ra1ra1	30	0	30
12	WF9R x ra1ra1	31	0	31
13	28-11/2-107 x ra1ra1	27	0	27
Totals		303	12	291

Cross no. 7 (PRV 30-71 x ra1ra1) included 47 plants. We obtained 12 plants that had ramosa type tassels and 35 that had normal tassels. The segregation for tassel type approximated a 3:1 ratio (Table 14). Assuming the same conditions previously given, the following genetic model was used to fit the observed ratios to the hypothesized genetic model for a 3:1 genetic ratio:

+ ral Qq x ralral qq (PRV 30-71)

↓

F_1 (3:1)	¼(+ ral Qq)	N
	¼(+ ral qq)	N
	¼(ralral Qq)	N
	¼(ralral qq)	ramosa

According to the Chi-square test:

$$[0.95 > P(X^2 \geq 0.007) > 0.90]$$

the proposed genetic model fits a 3:1 ratio. It seems that PRV 30-71 is another example supporting the conclusion that PRV 30 contains the ral gene in its genetic background.

Crosses no. 8 to no. 11, involving PRV 37, PRV 38, PRV 99, and PRV 216, were considered collectively because they do not include any ramosa type tassels in the F_1 generation (Table 14). The absence of ramosa expression in the F_1 generation could be explained with the situation of two alleles at one locus. For example:

++ (PRV) x ralral

↓

F_1 + ral N

Under this simple hypothesis, the four S_1 progenies representing the four PRVs involved in this set of crosses would not segregate for ramosa expression, and the F_2 generation would segregate in a ratio of 3 normal to 1 ramosa. All the previous cases, however, required a genetic model that

included a suppressor gene working with the ramosa expression. Hence, the following genetic model seems more reasonable:

$$+ \underline{ral}\ QQ \quad (PRV) \quad \times \quad \underline{ralral}\ qq$$

$$\downarrow$$

$$F_1 \qquad \begin{matrix} \tfrac{1}{2}(+\ \underline{ral}\ Qq) & N \\ \tfrac{1}{2}(\underline{ralral}\ Qq) & N \end{matrix}$$

With this model, the PRVs would have to include the ral gene which differentiates it from the previous model. If, in fact, the ral gene were present in the PRVs, we should obtain a ratio of 5.4 normal to 1 ramosa plants in the F_2, because the two F_1 genotypes would segregate in this manner:

$$\tfrac{1}{2}(+\ \underline{ral}\ Qq) \quad + \quad \tfrac{1}{2}(\underline{ralral}\ Qq) \qquad F_1$$

$$\downarrow \qquad\qquad \downarrow$$

$$\tfrac{1}{2}[1/16\ \underline{ralral}\ qq + 15/16N] + \tfrac{1}{2}[1/4\ \underline{ralral}\ qq + 3/4N] \qquad F_2$$

or

$$5/32\ \underline{ralral}\ qq + 27/32\ N$$

(1 ramosa:5.4 N)

The F_2 generations were intended to be produced in the Florida winter nursery in 1980-81, but for financial limitations, this goal was not achieved. For this set of crosses, we cannot extend our interpretations beyond the F_1 data.

Crosses no. 12 and no. 13 (Table 14) were a special case of two inbreds, WF9R and 38-11/2-107 (Plate 6), that were crossed with the homozygous source of the ramosa gene

(ralral). The results obtained in the F_1 crosses agree with what was expected from previous information about these inbreds. Both are parents of the female single-cross (WF9R x 38-11/2) (Plates 7 and 8) used to produce double-cross, HB19 (Plate 10), a hybrid used in northern Portugal. These inbreds are modified white versions of the original WF9 and 38-11 inbred lines. They were obtained by crossing each of them to the fasciated Portuguese germplasm with several backcrosses to the recurrent parent. With such a breeding program, it was possible to increase substantially the kernel-row number an average of 21 for the female single-cross (Appendix Table A10, entry 44; Plate 9) and an average of 18 for the double-cross (Appendix Table A10, entry 46; Plates 10 and 11). At the same time, due to the genetic background of the inbred 38-11, it was also possible to obtain good kernel depth in the single (14.2 mm for the female single-cross; Plate 9) and double-cross hybrids. As inbreds in advanced generations of inbreeding (more than eight), there were never any ralral plants in the F_1 generation, which is also evidence of no allelism between ramosa and fasciated genes.

Finally, another set of data will be considered both in relation to the ramosa and fasciation expression. These data will be for PRV 30-56, one of the most extreme cases for fasciation expression. PRV 30-56 was chosen because

adequate data were available for fasciation classification in several different progenies. There also was evidence that PRV 30-56 possessed the ral gene, which suggests, in our studies, that a relation occurs between the ramosa and fasciation expressions.

Considering first the ramosa expression of the data given in Table 12, 20 of 98 S_1 ears had the ralral phenotype. These data were confirmed for other data taken in the field for tassel classification before harvest; 23 S_1 plants were classified as having ralral tassels and 93 S_1 plants of 116 possible plants had normal tassels. A genetic model that would account for the 1:4 S_1 generation, and no ramosa plants in the F_1 generation, was explored. To explain these two conditions, we need to consider a more complex genetic model that includes the suppressor gene (Q) and also a masking gene (Q_m), which would overcome Q when it is in the dominant condition.

Hence:

S_0 - + ral Qq Q_m q_m (PRV 30-56)

$\downarrow$

S_1 - 13/64 ramosa + 51/64 N

According to this model, the 13 genotypes of the 64 possible that would have the ramosa (ralral) expression would include the following genotypes:

1 - ral ral QQ $Q_m Q_m$

2 - ral ral QQ $Q_m q_m$

2 - ral ral Qq $Q_m Q_m$

4 - ral ral Qq $Q_m q_m$

2 - ral ral qq $Q_m q_m$

1 - ral ral qq $q_m q_m$

1/13 - ral ral qq $Q_m Q_m$

This model fits the observed frequencies for the two sets of S_1 data and no ramosa (ral ral) plants in the F_1 when crossed with the ra3 source (Table 12). The same model was used to fit the F_2 data, but the predicted values did not give a good fit to the observed values. We had two ramosa plants out of 61, which was a ratio of about 1:30. It should be reemphasized, however, that the data at harvest sometimes failed to account for the total number of ral ral ears because of smut damage of the ears.

In my studies of PRV 30-56, I found this particular plant to breed true for fasciation expression in the S_1 progenies, and also segregating for ral ral expression in the F_2 generation when crossed with the ra3 source. This suggests that we can have a situation of both fasciated and ramosa (ral) genes interacting in their expression. The phenotype of a ral ral fasciated plant has been shown in my studies to be ramosa (ral ral). This suggests that the ral ral expression has a preferential segregation over fasciation.

Table 15 includes a set of data for fasciation expression on PRV 30-56 progenies. Examples of the level of fasciation expressed for a set of F_1 crosses of + ra3 x PRV 30-56 are shown in Plates 25 and 26. Two sets of ears were chosen to produce the F_2 generations: one included three fasciated ears and the other included two normal type ears (Table 15). These data provide possible speculation for the genetic differences found in their offspring. Another important division in Table 15 is concerned with two different types of crosses in which PRV 30-56 was involved: (1) crosses with the ra3 ramosa source, and (2) crosses with the inbred A632. From the cross with A632, we only have data for the F_1 generation, whereas for the cross with ra3 source, we also have data for the F_2 generation.

a. PRV 30-56 (S_1) x A632 This cross was produced using the S_1 seed of PRV 30-56 and a genetic model is outlined to interpret the data shown in Table 15 (F_1s, b). The data from Table 15 can be summarized as:

Fasciation classes	1	2	3	4	5	6	7	8	9
Number of ears				32	5	10	6	12	27
				32					27
					47			45	

In our first approach to obtain a genetic model, we will consider an approximate ratio of 1:1 in the F_1 generation, as was shown above.

Table 15. Data obtained for S_1, F_1, and F_2 generations of PRV 30-56 for fasciation expression

Sources[a]	Fasciation intensity, classes									Total ears, no.
	1	2	3	4	5	6	7	8	9	
S_1s	20	3	63	11	1	0	0	0	0	98
F_1s (a)	0	0	7	1	2	0	2	1	1	14
F_1s (b)	0	0	0	32	5	10	6	12	27	92
F_2s (c)	1	1	9	13	4	3	4	2	0	37
F_2s (d)	1	4	2	3	2	3	2	1	5	23
										264

[a](a) F_1s from the cross + ra3 x PRV 30-56 (grown at Ames); (b) F_1s from the cross PRV 30-56 x A632; (c) F_2s from 3 fasciated F_1 ears; (d) F_2s from 2 normal type F_1 ears.

Hence,

fa fa Uu (PRV 30-56)

S_1s ¼(fa fa UU) ½(fa fa Uu) ¼(fa fa uu) x Fal Fal uu (A632)

F_1 4/8(Fal fa Uu) + 4/8(Fal fa uu)

[1 fasciated (F) : 1 normal (N)]

According to this model, fasciation expresses itself in the recessive condition (fa fa) and U would be a suppressor gene of the fasciation expression when dominant. The resultant "two-peak" distribution in the F_1 generation is clearly seen in Figure 12a, A.

b. PRV 30-56 x ra3 A photographic coverage of the parental stage, S_1 progenies, F_1 crosses (from Florida and Ames) and F_2 generations are shown in Plates 23 to 31. Data for the F_1 cross are shown in Table 15 (F_1s, a) and can be summarized as:

Fasciation classes	1	2	3	4	5	6	7	8	9
Number of plants	0	0	7	1	2	0	2	1	1
		7		7					
		Fasciated		Intermediate: from slightly fasciated to normal type					

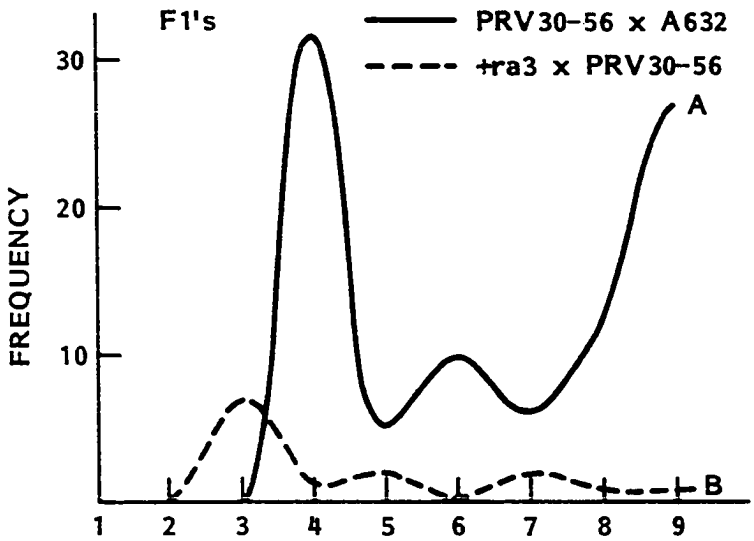
A genetic model was developed to interpret the different ratios in each generation, assuming a partial dominance situation.

Figure 12. Fasciation distribution in the F_1 and F_2 generations from the crosses between PRV 30-56 with A632 and + ra3

(a) Distribution patterns of the F_1 generations for the cross PRV 30-56 x A632 (A) and + ra3 x PRV 30-56 (B)

(b) F_2 generation distribution originated from two normal type F_1 ears (A) and from three fasciated type F_1 ears (B)

(a)


F1's
PRV30-56 x A632
+ra3 x PRV30-56
A
B
FREQUENCY
30
20
10
1
2
3
4
5
6
7
8
9

(b)

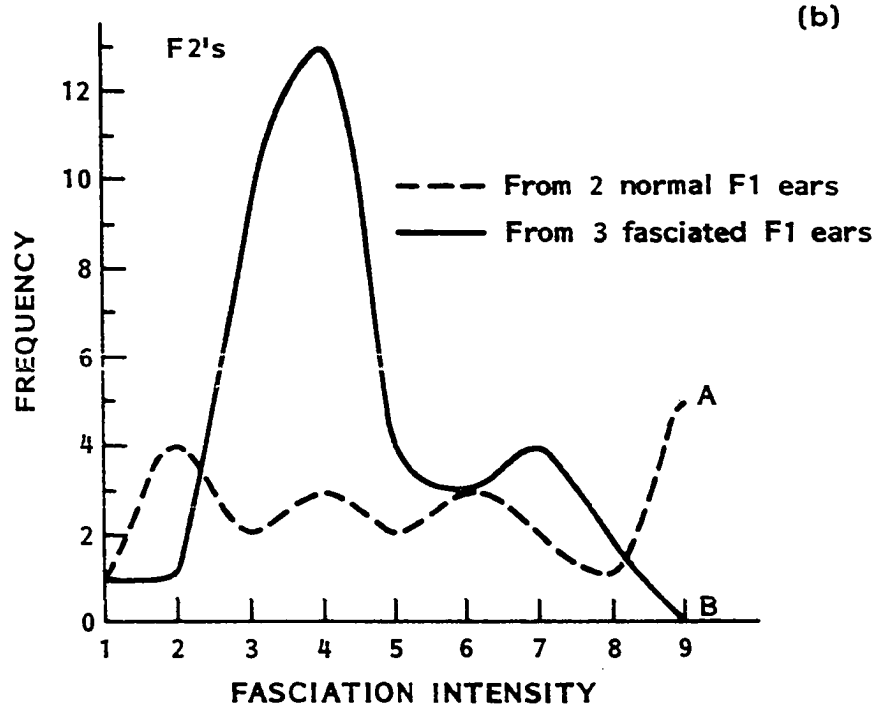
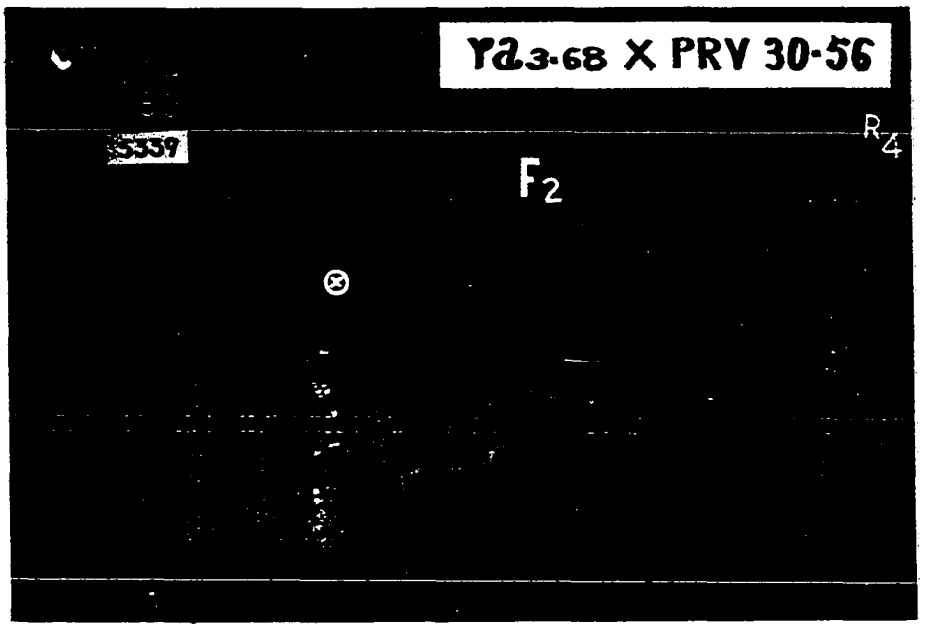

F2's
From 2 normal F1 ears
From 3 fasciated F1 ears
A
B
FREQUENCY
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
FASCIATION INTENSITY

Plate 28. F_2 segregation from an F_1 ear rated 4 for fasciation expression for the cross between the heterozygous ramosa 3 source (+ ra3) and PRV 30-56

Plate 29. F_2 segregation from an F_1 ear rated 4 for fasciation expression for the cross between the heterozygous ramosa 3 source (+ ra3) and PRV 30-56


Yd3-68 X PRV 30-56
5339
F2
R4

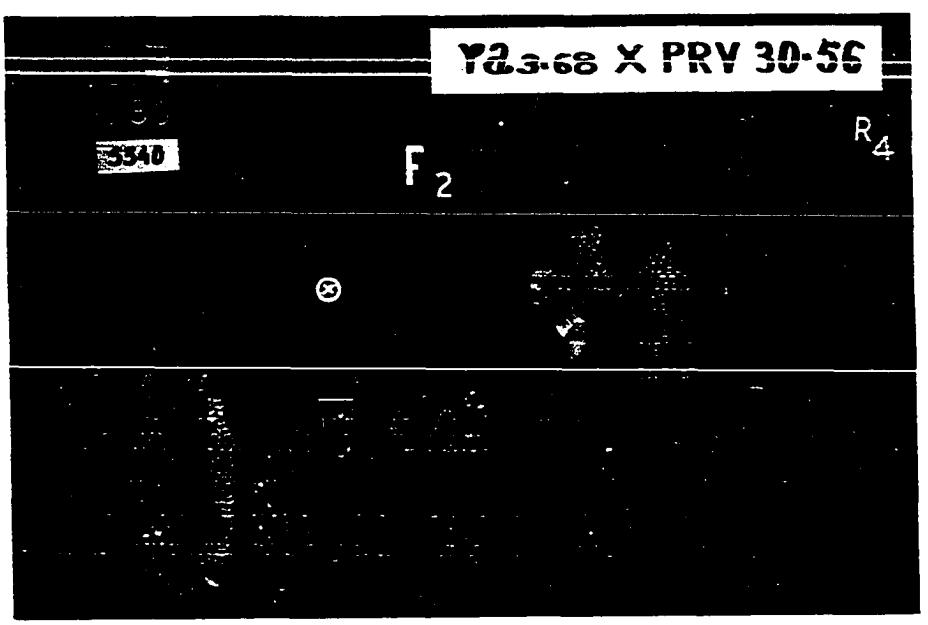
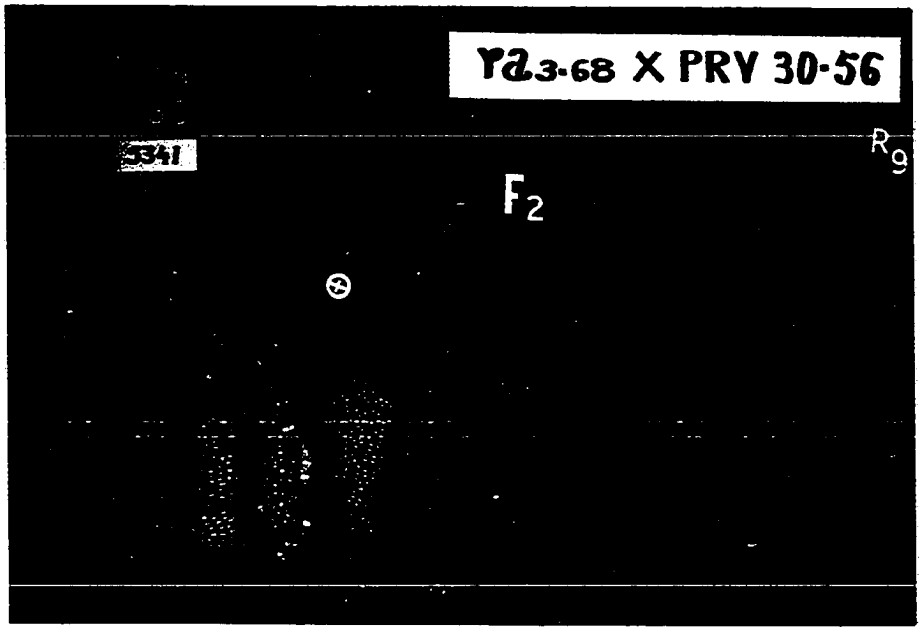
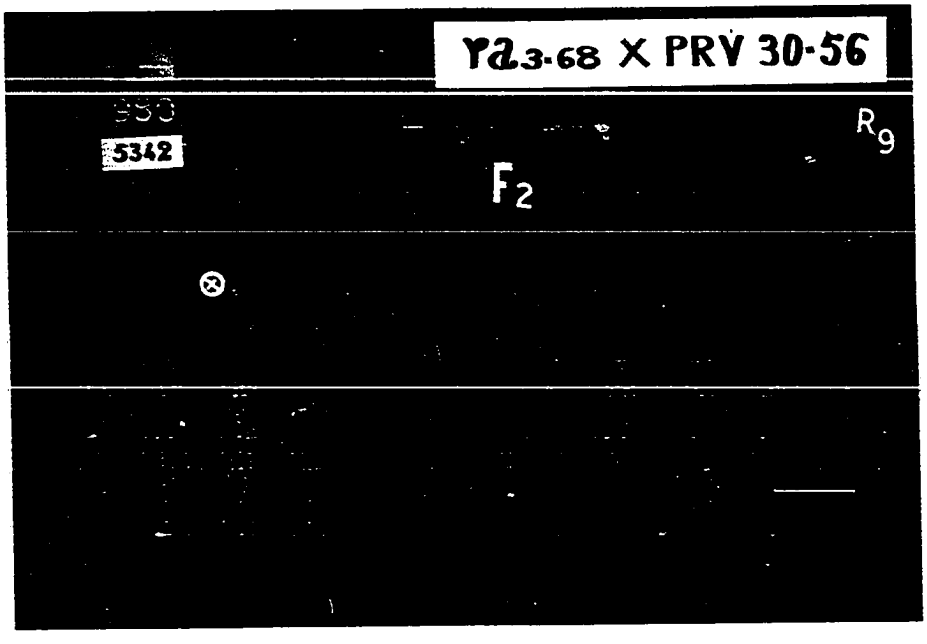

Yd3-68 X PRV 30-56
5340
F2
R4

Plate 30. F_2 segregation from an F_1 ear rated 9 for fasciation expression for the cross between the heterozygous ramosa 3 source (+ ra3) and PRV 30-56

Plate 31. F_2 segregation from an F_1 ear rated 9 for fasciation expression for the cross between the heterozygous ramosa 3 source (+ ra3) and PRV 30-56


Yd3-68 X PRV 30-56
5341
R_9
F_2


Yd3-68 X PRV 30-56
5342
R_9
F_2

My first approach for the PRV 30-56 x ra3 model was:

Fa2 Fa2 uu x fa fa Uu
(ramosa ra3 source) | (PRV 30-56)
↓

F_1 ½(Fa2 fa Uu) - fasciated (F)
½(Fa2 fa uu) - ± normal/± fasciated
[1 : 1]

For this model, Fa2 was partially dominant over the fa. We are including a new factor of partial dominance in our model. Figure 12a, B shows the distribution of the F_1 cross of PRV 30-56 x +/ra3.

Two sets of F_2 segregating populations were formed from these F_1 crosses: one from the normal type F_1 ears (Fa2 fa uu) and the other from the fasciated F_1 ears (Fa2 fa Uu). I will discuss each respective F_2 generation separately.

The first case is represented in Figure 12b, A.

F_1 - Fa2 fa uu - ± normal (intermediate)
↓

F_2 - ¼(Fa2 Fa2 uu) + ½(Fa2 fa uu) + ¼(fa fa uu)
normal intermediate fasciated

Data from Table 15 (F_2s, d) can be summarized in this form:

Fasciation classes	1	2	3	4	5	6	7	8	9
Number of plants	1	4	2	3	2	3	2	1	5
		6				11			5
		fasciated				intermediate			normal

This grouping of the data results in three classes that include 6 strongly fasciated, 11 intermediate, and 5 normal types. This model fits the observed values with a significant X^2 test.

$$[0.95 > P(X^2 \geq 0.1429) > 0.90]$$

The second case is represented in Figure 12b, B.

F_1 Fa2 fa Uu - fasciated

↓

F_2

Genotypes		Phenotypes	
1 - Fa2 Fa2 UU	-	"ff"	(fasciated)
2 - Fa2 Fa2 Uu	-	"ff"	(fasciated)
1 - Fa2 Fa2 uu	-	N	(normal)
2 - Fa2 fa UU	-	"ff"	(fasciated)
4 - Fa2 fa Uu	-	"ff"	(fasciated)
2 - Fa2 fa uu	-	f-	(slightly fasciated)
1 - fa fa UU	-	ff	(strongly fasciated)
2 - fa fa Uu	-	ff	(strongly fasciated)
1 - fa fa uu	-	ff	(strongly fasciated

We have, therefore, in the F_2 generation of the cross of PRV 30-56 x ra3, the following ratio:

4/16(ff) + 9/16("ff") + 2/16 (f-) + 1/16 (N)

This ratio agrees with the observed values listed in Table 15 (F_2s, c):

Fasciation classes	1	2	3	4	5	6	7	8	9
Number of ears	1	1	9	13	4	3	4	2	0
		10		20			4	2	
		(ff)		("ff")			(f-)	(N)	

The proposed model agrees very closely with the observed values, as shown by X^2 test:

$$[0.995 > P(X^2 \geq 0.0864) > 0.99]$$

This model for fasciation expression of PRV 30-56 also agrees with the data for the S_1 progenies. The selfs of PRV 30-56 bred true for fasciation (Table 15). This agrees with the genetic model of fa fa Uu.

Probably one of the most important observations that supports the suggested genetic model was its relationship with the distribution shown in Figure 12b, B. As we proceed in complexity of genetic models to explain our observed values, we obtain distributions that tend to approach a normal curve. This agrees with the data included in Table 16, where we had a test for the influence of the environment over the F_1 crosses. In both environments (Florida and Ames), the most

Table 16. Expression of fasciation of the F_1 crosses when grown at two different environments

Environment	Fasciated ears[a]	Intermediate ears[b]	Normal ears[c]	Total number of F_1 plants
Florida (1979-80)	62 (18.1%)	41 (12.0%)	239 (69.9%)	342
Ames (1980)	74 (18.5%)	163 (40.9%)	162 (40.6%)	399

[a]We included in this group all the ears classified from 1 to 4. A scale ranging from 1 (ralral ramosa expression) until 9 (normal type expression) was used.

[b]This group includes the ears classified between 5 and 8.

[c]Ears with a normal phenotypic expression (9).

extreme fasciated cases had the same percentage of expression, but when partial dominance was considered for the intermediate cases, there seems to be a strong environmental effect. Collectively, the different sources of information suggest the three classic conditions of a trait that behaves in a quantitative manner:

1. Several genes seemed to be involved in the expression of the trait;
2. Each gene has a small effect in the expression of the trait; and
3. Expression of the trait is influenced by the

environment in which it is measured.

The genetic analyses of the expression of ramosa and fasciation in my materials can be summarized as follows:

1. There was no evidence of allelism between genes responsible for the ramosa and fasciation characters.
2. There was some evidence that both the expression of ramosa 1 gene (ra1) and of fasciation was conditioned by some suppressor genes in the dominant condition.
3. There was no evidence of dominant fasciation in PRV 30. A test of dominance was conducted in crosses between several PRVs (including PRV 30) and the inbred A632 (Table 17). Although some cases suggested dominance, it seemed that the action of suppressor genes caused the F_1 crosses to behave as dominant genes. However, when we consider the S_1 segregations, the hypothesis of dominance was not supported.
4. The different attempts to fit genetic models suggested that the fasciation expression was a very complex trait with situations that cover a very diversified range in levels of expressivity that were highly influenced by the environment; the inheritance of fasciation was not simple. My data

Table 17. Set of crosses between the inbred A632 and some PRVs with a strong expression of fasciation

Pedigree		Prog.[a]	Fasciation intensity, classes								
			1	2	3	4	5	6	7	8	9
PRV 30-56 x A632		F_1	0	0	7	1	2	0	2	1	1
		S_1^1	20	3	63	11	1	0	0	0	0
PRV 37-13 x A632		F_1	0	0	0	3	4	6	3	12	66
		S_1	1	0	0	5	5	0	0	0	0
PRV 38-61 x A632		F_1	0	0	0	3	2	3	8	19	75
		S_1	0	0	4	3	0	0	0	0	0
PRV 214-18 x A632		F_1	0	0	0	0	0	2	2	5	77
		S_1	0	0	1	0	1	0	0	0	0
PRV 216-9 x A632		F_1	0	0	0	0	1	0	0	0	102
		S_1	0	0	1	1	2	0	0	2	0
38-11/2-19 x A632		F_1	0	0	0	1	0	2	0	0	102
		S_1	0	0	1	3	2	0	0	0	0
38-11/2-39 x A632		F_1	0	0	0	2	3	3	0	3	95
		S_1	0	0	1	6	1	0	0	1	4
Totals	618	F_1	0	0	7	10	12	16	15	40	518
	150	S_1	21	3	78	29	12	0	0	3	4

[a]The S_1s are referred to the respective PRV female parent in each cross.

suggested that fasciation was inherited in a quantitative manner.

B. Quantitative Genetics Approach

1. S_1 progenies

Table A7 in the Appendix includes the list of entries and respective pedigrees evaluated in the S_1 progeny trials in 1981. The combined analysis of variance over environments is presented in Table 18. Data from Table 18 show:

1. There were highly significant differences ($P \leq 0.01$) for the environmental source of variation. This evidence supports previous conclusions of the influence of the environment for the fasciation expression in PRV 30 germplasm.
2. There were highly significant differences among genotypes for all traits considered.
3. For the interaction source of variation (G*E), there were highly significant differences for all traits, except for ear diameter D_4 and D_6, and for stand (STD). For D_4 and D_6, the mean squares were not significantly different from zero, and for STD, the G*E source of variation was significant at the 95% level of probability. This suggests that D_4 and D_6 were the most stable parameters.
4. Heritabilities (broad sense) estimates, on a progeny

Table 18. Combined analysis of variance for 12 traits of the 100 S_1 progenies evaluated at two environments in 1981

Source of variation	df	Mean squares[a]				
		FA	D_1	D_3	D_5	D_2
Environments (E)	1	27.08**	4.05**	2.16**	2.18**	5.63**
Reps/E	4	0.13	0.03	0.03	0.02	0.03
S_1 progenies (G)	99	9.16**	0.61**	0.76**	1.04**	0.46**
G*E	99	0.60**	0.04**	0.04**	0.07**	0.03**
Error	396	0.35	0.02	0.02	0.03	0.02
Total	599					
Means		6.75	4.08	4.06	3.64	3.78
CV (%)		8.82	3.80	3.88	5.04	3.82
h^2 (%)[b]		93	94	95	94	93

[a]The trait designations are FA = fasciation; D_1, D_3, D_5, D_2, D_4, D_6 = ear diameters, R_1, R_2 = kernel-row numbers; L = ear length, STD = stand count; and Y = yield.

[b]Heritability (broad sense) estimated on a progeny mean basis as:

$$\hat{\sigma}^2_g/(\hat{\sigma}^2_{re} + \hat{\sigma}^2_{ge}/e + \hat{\sigma}^2_g) \ .$$

*,**Significant at the 5 and 1% levels of probability, respectively.

Mean squares						
D_4	D_6	R_1	R_2	L	STD	Y
1.74**	1.24**	45.65**	63.17**	43.25**	36.51**	14408800.67**
0.02	0.01	0.29	0.37	0.69	2.78	30758.04
0.37**	0.30**	14.28**	20.88**	12.54**	10.11**	723482.96**
0.02	0.01	1.15**	1.68**	1.25**	4.26*	149985.52**
0.01	0.01	0.69	0.88	0.83	3.11	68829.46
3.71	3.24	16.27	16.16	12.37	16.01	1058.98
3.21	3.66	5.12	5.82	7.38	11.02	24.77
95	95	92	92	90	58	79

mean basis, exceeded 90% for all traits, except for STD (58%) and yield (79%). These high heritability estimates suggest that the traits under consideration could be effectively selected under selection methods using S_1 progeny means.

Figures 13 to 18 show the distribution patterns and ranges of values for the different traits evaluated in the S_1 progeny trials. The fasciation expression in the S_1 progenies (Figure 13a) shows a distribution pattern that is similar to normal distribution. The same pattern occurs for ear length (L), as shown in Figure 13b.

Figures 14a and 14b show the first pair of alternate ear diameters, D_1 and D_2 (see Figure 2). The distribution patterns are very similar for both D_1 and D_2; both have a normal distribution with a very slight skewness to the left, suggesting some partial dominance may be involved in the expression of these two traits.

Figures 15a and 15b show the distribution patterns for diameters D_3 and D_4. These distributions look very similar to those for D_1 and D_2 shown in Figures 14a and 14b. There is a slight skewness to the left, suggesting some partial dominance for the expression of D_3 and D_4.

Figure 16a shows the distribution of the ear diameter D_5. The distribution for D_5 shows a pronounced skewness to the left, suggesting dominance was involved for smaller

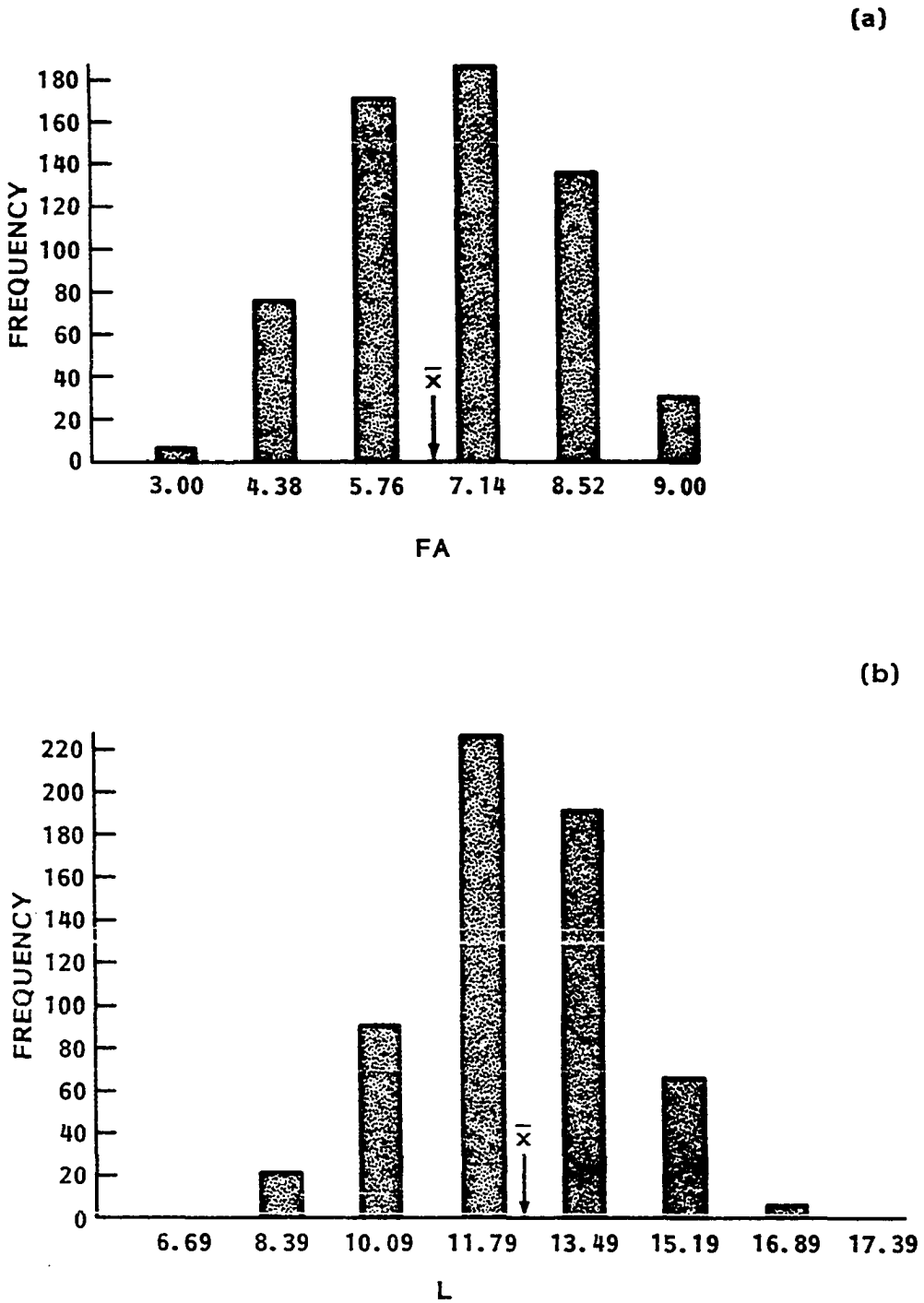


Figure 13. Distribution of (a) fasciation expression, FA, and (b) ear length, L, in the S_1 progeny trials

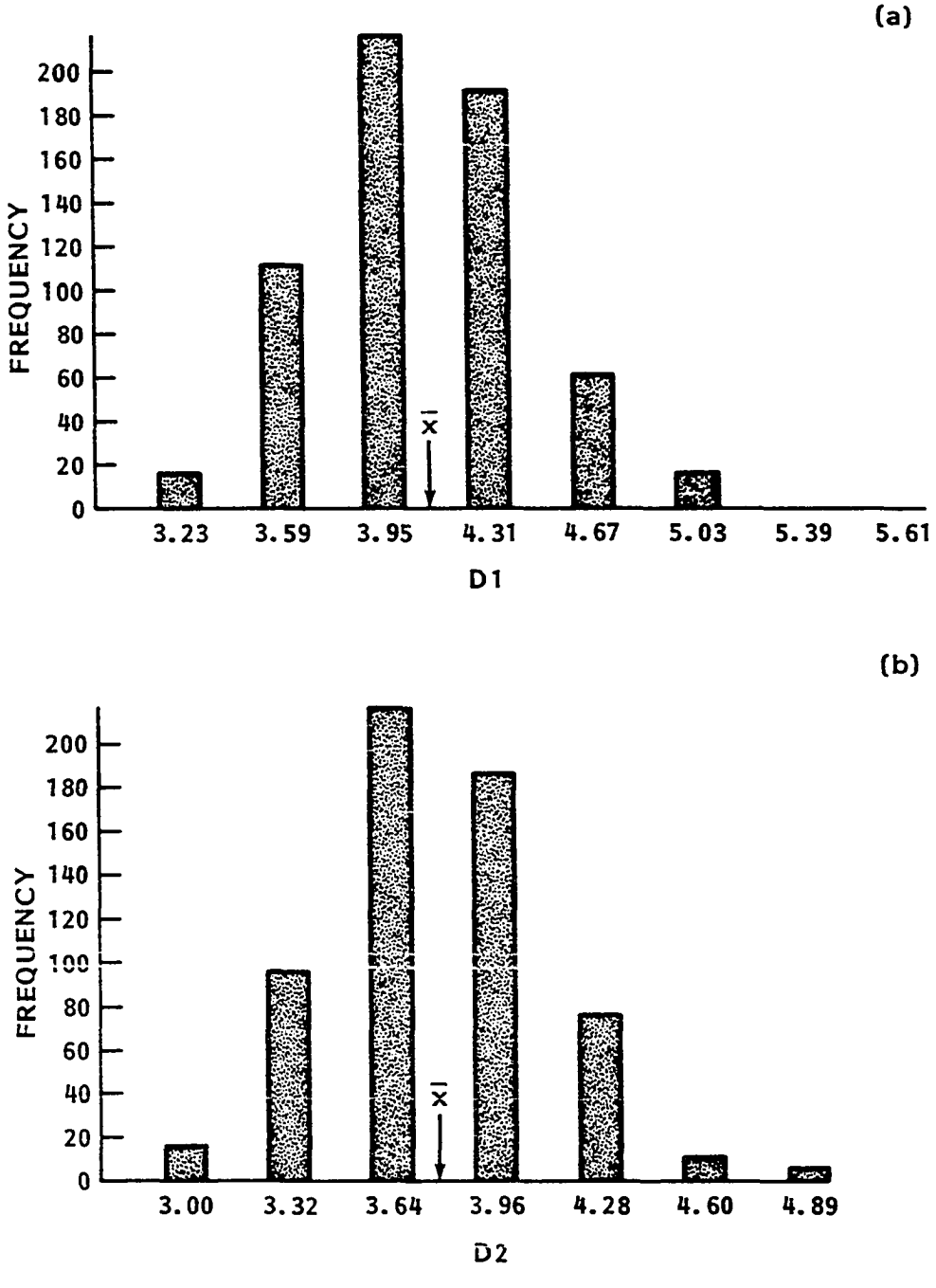


Figure 14. Distribution of the alternate ear diameters, (a) D_1 and (b) D_2, in the S_1 progeny trials

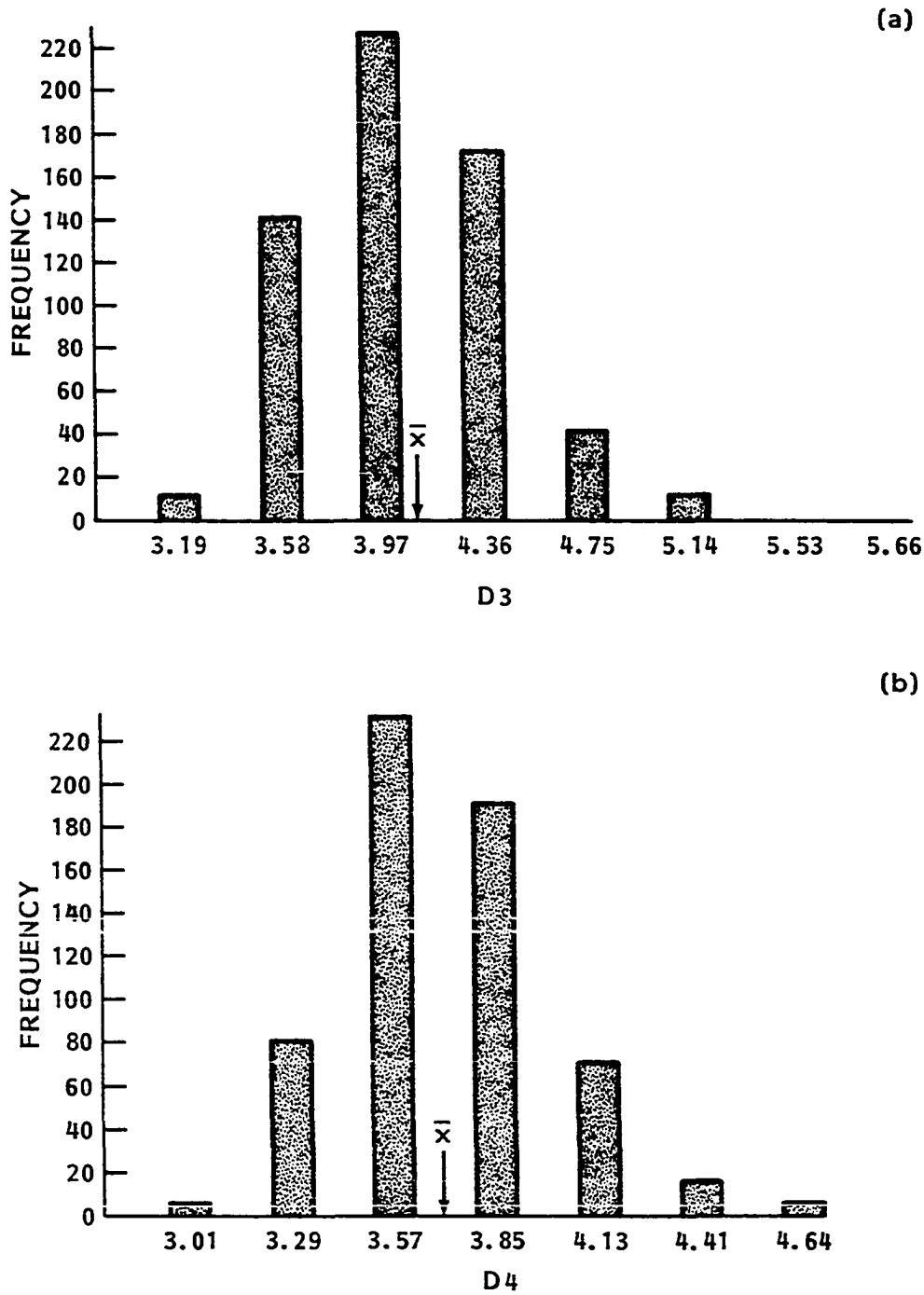


Figure 15. Distribution of the alternate ear diameters, (a) D_3 and (b) D_4, in the S_1 progeny trials

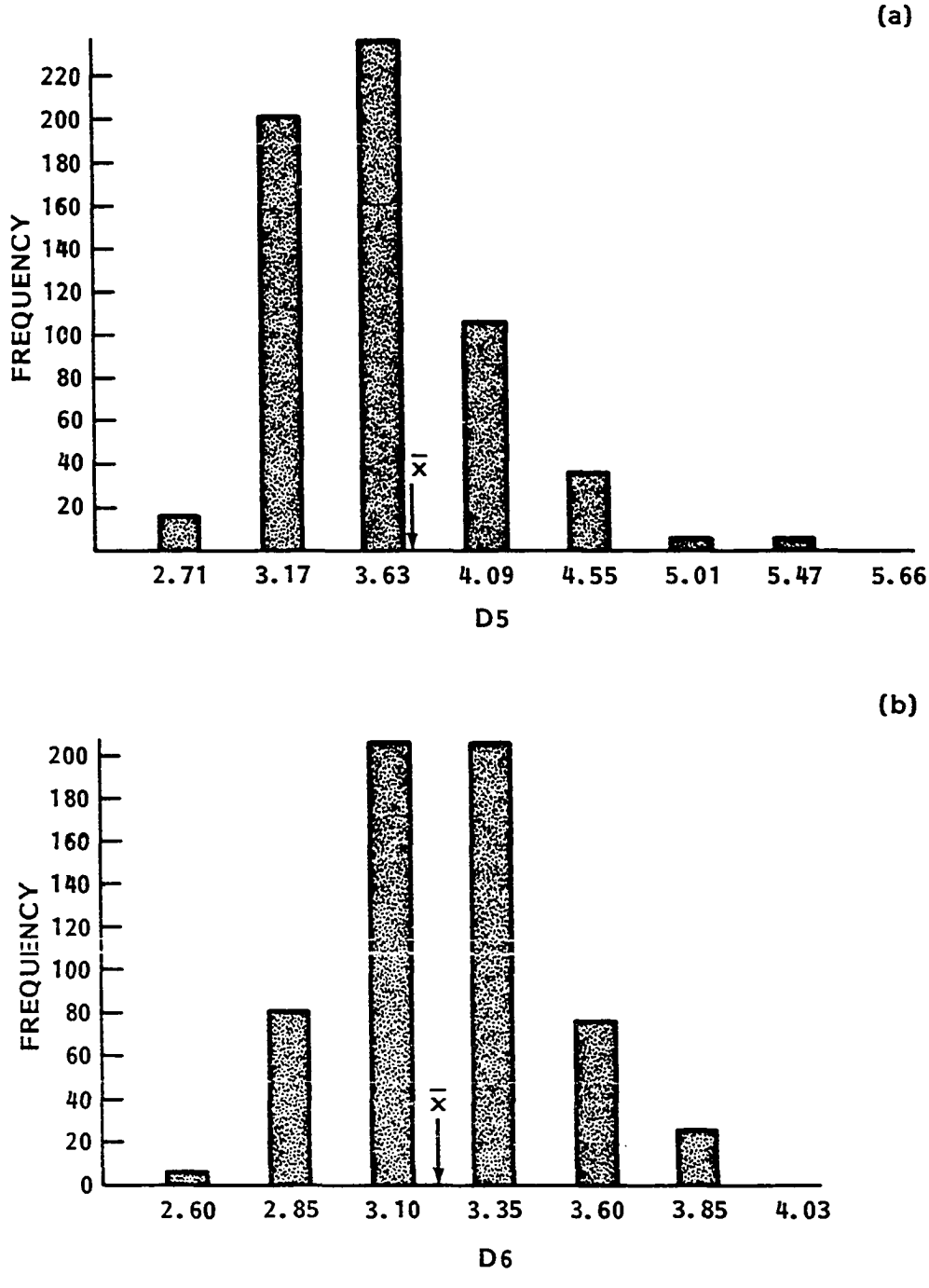


Figure 16. Distribution of the alternate ear diameters, (a) D_5 and (b) D_6, in the S_1 progeny trials

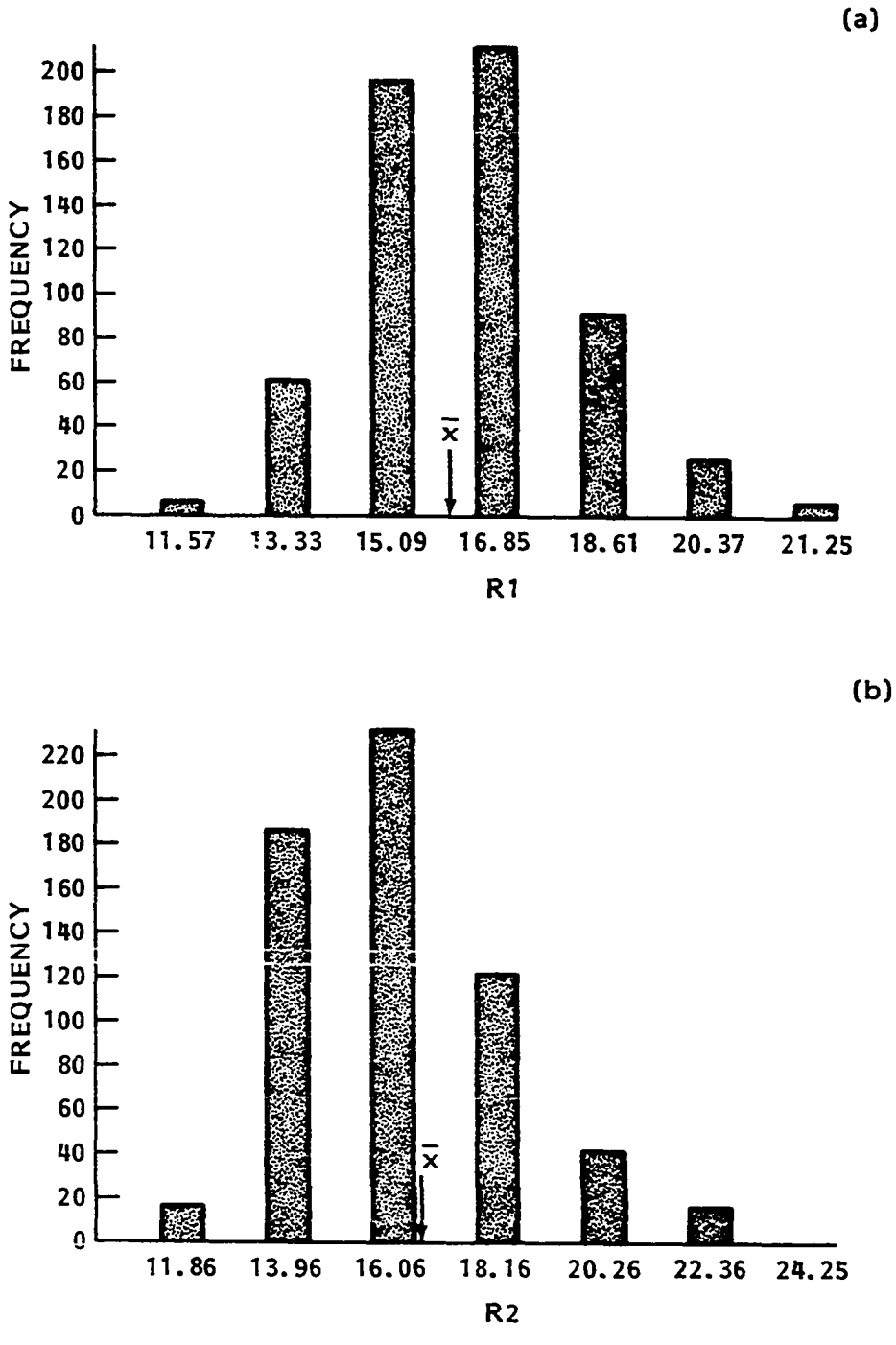


Figure 17. Distribution of kernel-row numbers (a) R_1 and (b) R_2 in the S_1 progeny trials

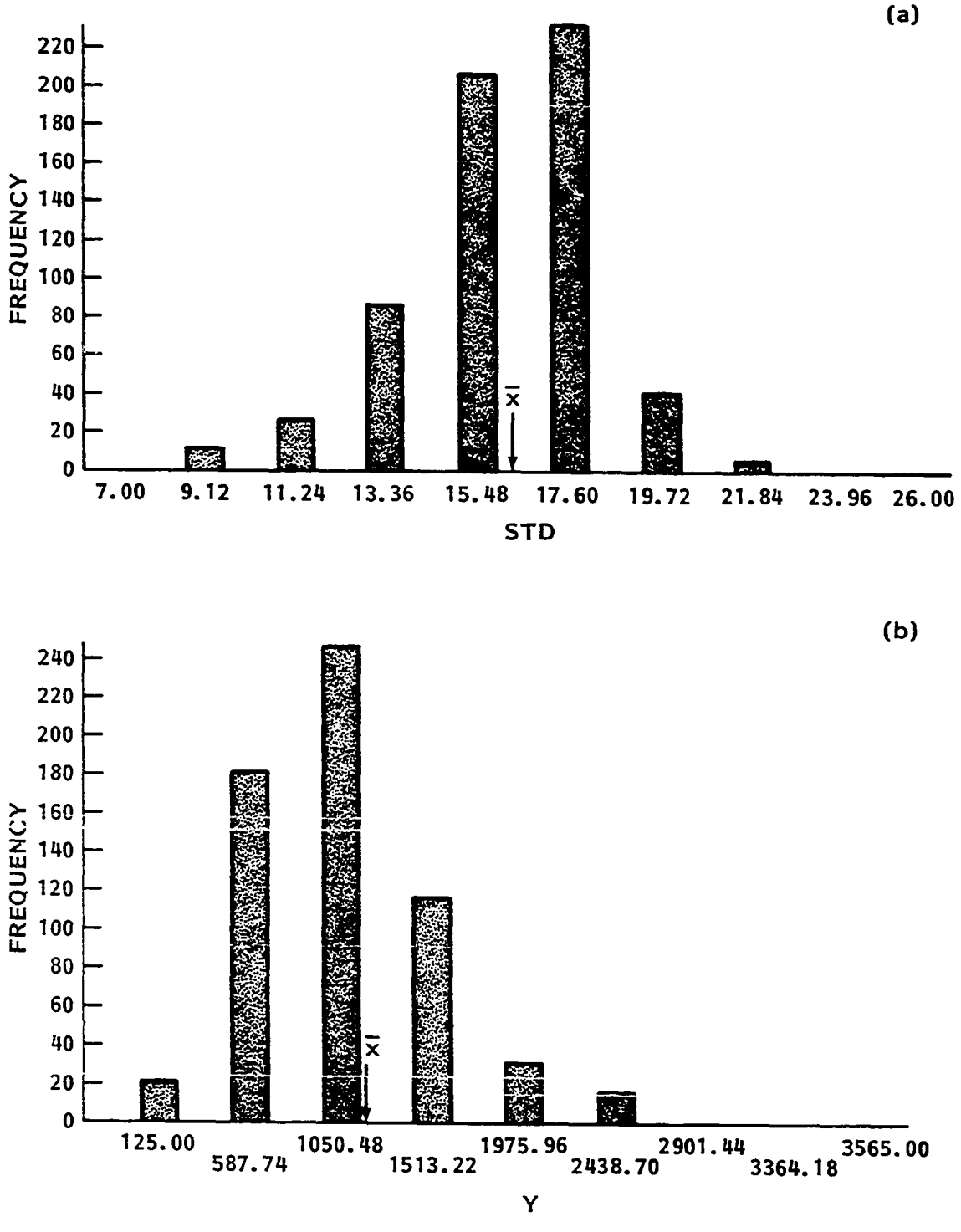


Figure 18. Distribution of (a) stand count, STD, and (b) yield, Y, in the S_1 progeny trials

diameters in this position of the ear. The distribution of its alternate diameter D_6 is shown in Figure 16b; the D_6 distribution approaches the normal distribution pattern.

Figure 17 shows the distribution of the two kernel-row counts (R_1 and R_2). R_1 distribution (Figure 17a) shows a close approach to a normal distribution, while R_2 distribution (Figure 17b) shows a slight skewness to the left, suggesting partial dominance was present for fewer kernel-row numbers. Figure 17 also shows a greater range of values for R_2 than for R_1.

Finally, Figure 18 represents the pattern distribution for stand count (STD, Figure 18a) and for yield (Y, Figure 18b). Figures 18a and 18b have a pronounced skewness, but in opposite directions. While the STD skewness is to the right, the skewness of yield is to the left, suggesting that partial dominance in opposite directions was involved in the expression of these two traits.

The distribution patterns for all traits approached normal distributions, which are the basic premises for the quantitative analysis of a trait. Yield is usually considered as a trait whose expression is determined in a quantitative manner. The distributions of the other traits were similar to that for yield. This supports our previous conclusions of the quantitative expression of traits involved in fasciation expression.

Table 19 includes the phenotypic and genotypic correlation coefficients among all traits, except for stand count (STD). Table 19 shows:

1. Phenotypic and genotypic correlation coefficients were very similar for all traits.
2. Fasciation expression (FA) was (a) positively correlated ($P < 0.05$) with ear length ($r=0.24^*$) and yield ($r=0.24^*$) and (b) negatively correlated ($P < 0.01$) with all other traits. It should be emphasized, however, that the lowest values attributed to fasciation expression correspond to the strongest expressivity of the character (and vice versa); hence, the correlations shall be interpreted accordingly.
3. Ear diameter D_1 was negatively correlated with fasciation expression ($r=-0.54^{**}$), but positively correlated with all other parameters, except for ear length and yield.
4. Ear diameters D_3, D_5, D_2, and D_4 were negatively correlated with fasciation expression and highly correlated with all other traits, except with ear length and yield. Among these diameter traits, D_2 had the highest correlations, but D_2 was not significantly correlated with L and Y; there was, however, a small positive trend.

Table 19. Phenotypic and genotypic (in parentheses) correlation coefficients between traits for the 100 S_1 progenies evaluated in 1981

Traits	Traits[a]			
	D_1	D_3	D_5	D_2
FA	-0.54** (-0.56)	-0.77** (-0.86)	-0.82** (-0.84)	-0.36** (-0.38)
D_1		0.90** (0.91)	0.79** (0.81)	0.95** (0.95)
D_3			0.95** (0.96)	0.79** (0.80)
D_5				0.68** (0.69)
D_2				
D_4				
D_6				
R_1				
R_2				
L				

[a]The trait designations are as follows: FA, fasciation; D_1, D_3, D_5, D_2, D_4, D_6, ear diameters; R_1 and R_2, kernel-row numbers; L, ear length; and Y, yield.

*,**Significant at the 5 and 1% probability levels, respectively.

Traits					
D_4	D_6	R_1	R_2	L	Y
-0.46** (-0.47)	-0.48** (-0.49)	-0.71** (-0.74)	-0.84** (-0.86)	0.24* (0.26)	0.24* (0.27)
0.90** (0.91)	0.83** (0.84)	0.61** (0.62)	0.53** (0.54)	-0.02 (-0.05)	0.06 (0.04)
0.87** (0.88)	0.85** (0.86)	0.71** (0.72)	0.75** (0.75)	-0.05 (-0.07)	-0.04 (-0.07)
0.79** (0.80)	0.82** (0.83)	0.63** (0.65)	0.80** (0.80)	0.02 (0.01)	-0.02 (-0.04)
0.92** (0.93)	0.84** (0.85)	0.51** (0.52)	0.41** (0.42)	0.07 (0.04)	0.15 (0.13)
	0.96** (0.97)	0.53** (0.54)	0.51** (0.52)	0.16 (0.15)	0.13 (0.11)
		0.44** (0.44)	0.51** (0.51)	0.24* (0.24)	0.15 (0.15)
			0.88** (0.89)	-0.26** (-0.29)	-0.05 (-0.06)
				-0.12 (-0.14)	-0.02 (-0.03)
					0.49** (0.53)

5. Ear diameter D_6 was negatively correlated with fasciation expression (r=-0.48**), positively correlated with ear length (r=0.24*), and highly correlated with all the other traits, except with yield. With yield, however, there was an indication of a positive trend (r=0.15) for increased yield with greater ear diameter D_6.
6. Kernel-row number R_1 (see Figure 2), was negatively correlated with fasciation expression (r=-0.71**) and highly correlated with all ear parameters (D_1 to D_6) and kernel-row number R_2. R_1 was negatively correlated with ear length (r=-0.26**) and had no significant correlation with yield (r=-0.05).
7. Kernel-row number R_2 had no significant correlation with ear length (r=-0.12) and yield (r=-0.02). A slight negative tendency was shown for R_2 with both ear length and yield. R_2 was negatively correlated with fasciation expression (r=-0.84**), and positively correlated with all the other parameters.
8. Ear length was positively correlated with fasciation expression (r=0.24*), diameter D_6 (r=0.24*), and yield (r=0.49**). It was negatively correlated with kernel-row number R_1 (r=-0.26**), and no significant correlations were shown with the other traits.

The replicated yield trials of the S_1 progenies suggest that the most important traits in the S_1 progenies were ear length and ear diameter D_6. Ear length was the only trait that was positively correlated with yield (r=0.49**). Ear diameter D_6 was positively correlated with all the other traits, except yield, with which, however, it shows a positive trend.

Table 20 presents data from the multiple regression analysis of all traits on yield. Two traits, stand count (STD) and ear length (L), accounted for the greatest contribution (32.8%) to the sum of squares of the regression model. The maximum contribution to the regression sum of squares (47.2%) was attained with a model that included the following parameters by this order: L, STD, FA, R_2, D_3, D_1, and D_6. However, a simpler model including only five parameters (L, STD, D_2, FA, and R_2) accounted for 45.4% of the total regression sum of squares. Table 20 also shows the relative importance of each trait to the total regression sum of squares, indicating that the ear diameter D_2 was the third most important trait following L and STD. This indicates that, contrary to our previous conclusion suggested from Table 19, ear diameter D_2 was greater than D_6 in its relative importance for yield contribution. Hence, this suggests that, for the S_1 progenies, all the measurements taken could be reduced to only two traits: ear diameter D_2 and ear

Table 20. Multiple regression analysis of the S_1 progenies for the different traits included in model regressed on yield

Source (regression model)[a]	df	Sum of squares
L/Y	1	2899936.86
STD/Y	1	1011442.58
L STD/Y	2	3911379.44
D_2/Y	1	460677.36
D_2 L STD/Y	3	4372056.80
FA/Y	1	558954.78
FA D_2 L STD/Y	4	4931011.58
R_2/Y	1	488419.42
FA D_2 R_2 L STD/Y	5	5419431.00
D_3/Y	1	91226.40
FA D_3 D_2 R_2 L STD/Y	6	5510657.40
D_1/Y	1	54347.03
FA D_1 D_3 R_2 L STD/Y (D_2 replaced by D_1)	6	5564059.36
D_6/Y	1	69825.10
FA D_1 D_3 D_6 R_2 L STD/Y	7	5633884.46
D_5/Y	1	3961.68
FA D_1 D_3 D_5 D_6 R_2 L STD/Y	8	5637846.14
D_4/Y	1	675.99
FA D_1 D_3 D_5 D_4 D_6 R_2 L STD/Y	9	5638522.13
D_2/Y	1	945.07
FA D_1 D_3 D_5 D_2 D_4 D_6 R_2 L STD/Y	10	5639467.20
R_1/Y	1	21.39
FA D_1 D_3 D_5 D_2 D_4 D_6 R_1 R_2 L STD/Y	11	5639488.59
Error	88	6298008.75
Total	99	11937497.34

[a]The trait designations are FA, fasciation; D_1, D_3, D_5, D_2, D_6, ear diameters; R_1, R_2, kernel-row numbers; L, ear length; STD, stand count; and Y, yield.

Individual variables	R-square, %
L if alone	(24.3)
STD if after L	(8.5)
	32.8
D_2 if after L STD	(3.8)
	36.6
FA if after L STD D_2	(4.7)
	41.3
R_2 if after L STD D_2 FA	(4.1)
	45.4
D_3 if after L STD D_2 FA R_2	(0.8)
	46.2
D_1 if after L STD FA R_2 D_3 (D_2 replaced by D_1)	(0.4)
	46.6
D_6 if after L STD FA R_2 D_3 D_1	(0.6)
	47.2
D_5 if after L STD FA R_2 D_3 D_1 D_6	(0.0)
	47.2
D_4 if after L STD FA R_2 D_3 D_1 D_6 D_5	(0.0)
	47.2
D_2 if after L STD FA R_2 D_3 D_1 D_6 D_5 D_4	(0.0)
	47.2
R_1 if after L STD FA R_2 D_3 D_1 D_6 D_5 D_4 D_2	(0.0)
	47.2
	52.8
	100.0

length (L). Both traits approached a normal distribution in the S_1 progenies as seen in Figures 13b and 14b, indicating that ear diameter D_2 and ear length were inherited in a quantitative manner.

2. S_2 progenies

Table A8 (Appendix) describes the entries and respective pedigrees evaluated in the S_2 progeny trials conducted in 1981. Entries from 1 to 90 represent the S_2 progenies, and entries from 91 to 100 represent checks. Checks were divided into two sets: ramosa sources (entries 91 to 93), and others (entries 94 to 100). The set "others", was divided into two subsets: U.S. inbreds (entries 97 to 100) and rest (94 to 96).

Table 21 includes the analysis of variance of the S_2 progenies for the different traits evaluated. From Table 21, we have:

1. There were highly significant differences among all entries and among S_2 progenies for all traits evaluated.
2. There were significant differences ($P \leq 0.05$) between S_2 progenies and checks for stand count (STD), and highly significant differences ($P \leq 0.01$) for the other traits except for ear diameter D_1.
3. There were highly significant differences among checks for all traits.

Table 21. Analysis of variance of 90 S_2 progenies and 10 check entries, for fasciation expression (FA), six ear diameters (D_1 to D_6), two kernel-row numbers (R_1 and R_2), ear length (L), stand count (STD), and yield (Y)

Source	df	Mean squares				
		FA	D_1	D_3	D_5	D_2
Reps	2	0.81	0.03	0.06	0.31	0.03
Entries	99	7.42**	0.58**	1.05**	1.66**	0.40**
S_2 progenies	89	5.09**	0.62**	1.10**	1.73**	0.40**
S_2s vs checks	1	230.56**	0.01	2.94**	7.07**	2.09**
Checks	9	5.69**	0.27**	0.36**	0.37**	0.25**
Ramosa sources	2	5.12**	0.15*	0.04	0.03	0.13*
Ramosa vs others	1	2.02*	0.03	0.24*	0.40	0.02
Others	6	6.50**	0.35**	0.49**	0.47**	0.32**
U.S. inbreds	3	1.82**	0.60**	0.83**	0.71**	0.47**
Inbreds vs rest	1	13.09**	0.15	0.21*	0.40	0.27**
Rest	2	10.23**	0.06	0.12*	0.16	0.12*
Error[a]		0.35	0.04	0.04	0.14	0.03
Total[b]						
CV (%)		11.62	5.09	4.52	9.33	5.02
Means		5.13	4.05	4.33	4.02	3.56
S_2 means		4.84	4.05	4.36	4.07	3.54
h^2 (%)[c]		93	93	97	92	92

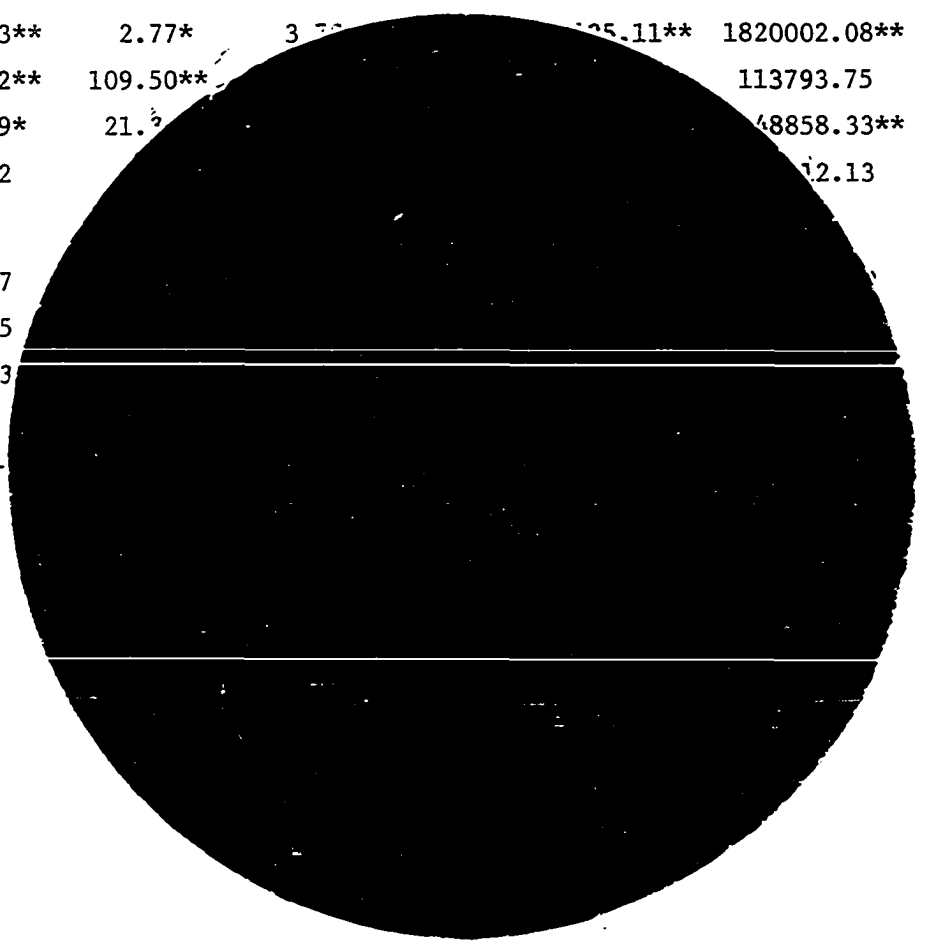
[a]Degrees of freedom for error are: 197 for traits D_1, D_3, D_5, D_2, D_4, D_6; 198 for traits FA, L, STD, and Y; and 193 for R_1 and R_2.

[b]The total degrees of freedom are: 298 for traits D_1, D_3, D_5, D_2, D_4, D_6; 299 for traits FA, L, STD, and Y; and 292 for R_1 and R_2.

[c]Heritabilities (broad sense) estimated as: $h^2 = \dfrac{\hat{\sigma}_g^2}{\frac{\hat{\sigma}^2}{r} + \hat{\sigma}_g^2}$;
with: $\hat{\sigma}_g^2$ = genotypic variance of S_2 progenies;
$\hat{\sigma}^2$ = error mean square; and
r = number of replications.

*,**Significant at the 5 and 1% levels, respectively.

Mean squares						
D_4	D_6	R_1	R_2	L	STD	Y
0.00	0.03	3.68*	9.37	0.05	8.41	70007.58
0.35**	0.35**	20.61**	47.26**	13.17**	30.77**	740507.39**
0.34**	0.34**	19.93**	47.90**	8.67**	26.94**	663402.69**
2.25**	1.20**	102.53**	238.32**	377.45**	17.60**	5473801.82**
0.28**	0.28**	18.06**	19.81**	17.22**	70.08**	977065.65**
0.01	0.04	1.06	2.22	7.35**	6.33	696808.33**
0.24**	0.35**	0.01	2.76	29.97**	46.41**	328457.50*
0.37**	0.35**	26.73**	28.51**	18.39**	95.27**	1178586.11**
0.61**	0.53**	2.77*	3		.11**	1820002.08**
0.33**	0.32**	109.50**				113793.75
0.03	0.09*	21.				48858.33**
0.02	0.02					2.13
4.04	4.47					
3.63	3.25					
3.60	3.23					
94	94					



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2.25**	1.20**	102.53**	238.32**	377.45**	17.60**	5473801.82**
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0.37**	0.35**	26.73**	28.51**	18.39**	95.27**	1178586.11**
0.61**	0.53**	2.77*	3.79	11.78**	125.11**	1820002.08**
0.33**	0.32**	109.50**	107.44**	7.77**	14.29*	113793.75
0.03	0.09*	21.30**	26.12**	33.61**	91.00**	748858.33**
0.02	0.02	0.99	4.70	0.75	3.43	59512.13
4.04	4.47	5.83	12.06	7.81	13.08	33.89
3.63	3.25	17.09	17.98	11.12	14.16	719.93
3.60	3.23	17.29	18.29	10.74	14.24	674.91
94	94	95	90	91	87	91

4. There were significant differences ($P \leq 0.05$) among ramosa sources for ear diameters D_1 and D_2; highly significant differences for fasciation expression (FA), ear length (L), and yield (Y) were detected; but no significant differences for ear diameters D_3, D_5, D_4, D_6, kernel row numbers R_1 and R_2, and stand count (STD).
5. Highly significant differences were found between ramosa sources and other checks, for ear diameters D_4 and D_6, ear length (L) and stand (STD). Significant differences ($P \leq 0.05$) were also found for the traits fasciation (FA), ear diameter D_3 and yield (Y). There were no significant differences for ear diameters D_1, D_5, and D_2 and kernel-row numbers R_1 and R_2.
6. Highly significant differences were found among "others" for all traits.
7. There were highly significant differences among U.S. inbreds for the traits fasciation (FA), for all ear diameters (D_1 to D_6), ear length (L), stand (STD), and yield (Y), and significant differences ($P \leq 0.05$) for kernel-row number R_1. No significant differences were found for kernel-row number R_2.
8. Comparing U.S. inbreds vs rest, we found highly significant differences ($P \leq 0.01$) for fasciation expression (FA), ear diameters D_2, D_4, and D_6, kernel-

row numbers R_1 and R_2, and ear length (L); significant differences ($P \leq 0.05$) were found for diameter D_3 and stand (STD); no significant differences for diameters D_1 and D_5, and yield (Y).

9. Among "rest", we found significant differences ($P \leq 0.05$) for ear diameters D_3, D_2, and D_6, and highly significant differences ($P \leq 0.01$) for fasciation (FA), kernel-row numbers R_1 and R_2, ear length (L), stand (STD), and yield (Y). No significant difference was found for ear diameters D_1, D_5, and D_4.

The distribution patterns and respective ranges for all the traits evaluated in the S_2 progenies trial are presented in Figures 19 to 24. For fasciation expression (FA), Figure 19a shows a distribution pattern with a pronounced skewness to the left, suggesting partial dominance was involved in fasciation expression among S_2 progenies. The distribution pattern for the S_2 progenies differs from the nearly normal distribution presented in Figure 13a for fasciation expression of S_1 progenies.

The S_2 progeny distribution for ear length (L) shows a pattern similar to that for S_1 progenies for the same trait (Figure 19b); that is, both distributions for ear length approximated a normal distribution.

Figure 20 represents the first pair of alternate

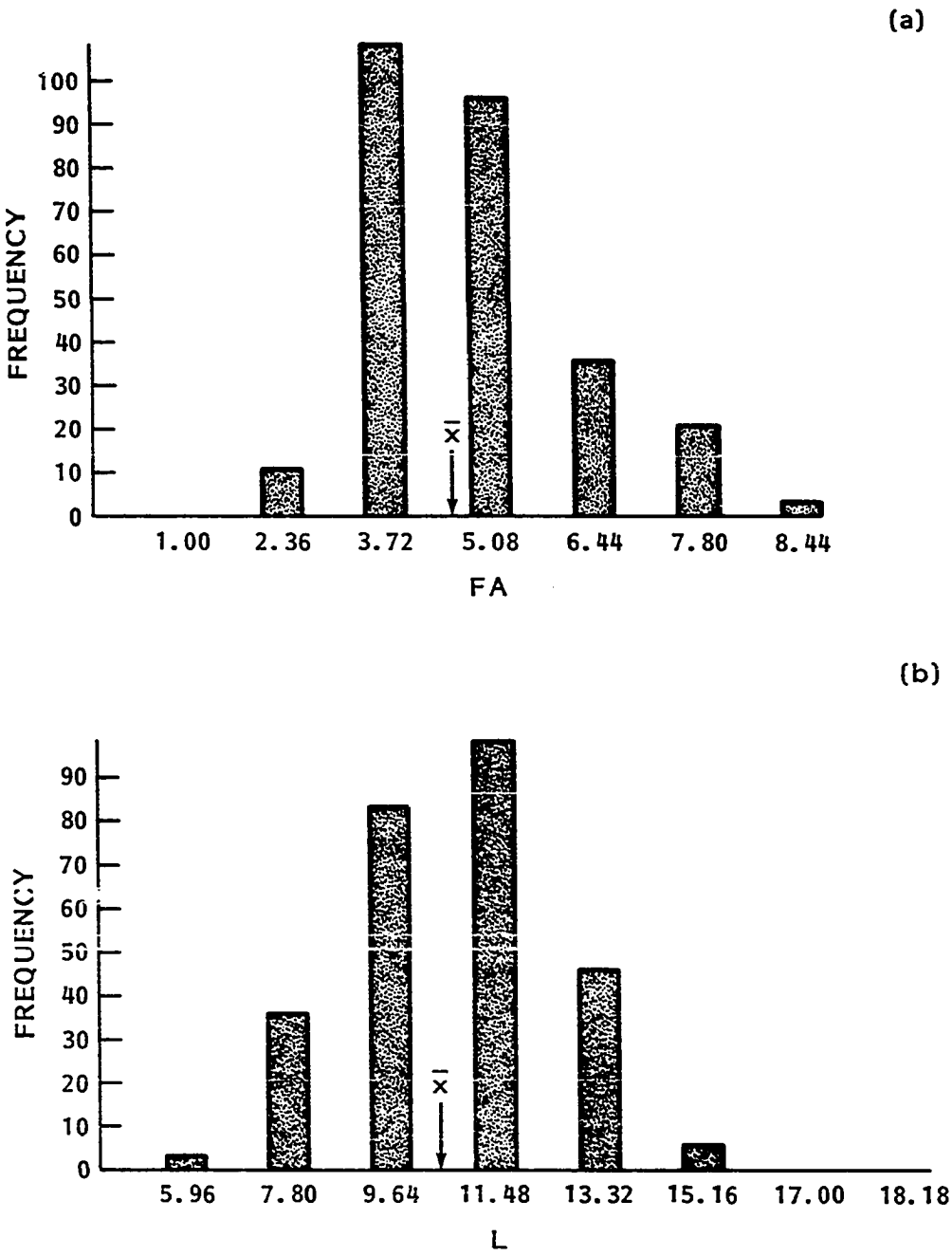

Figure 19. Distribution of (a) fasciation expression, FA, and (b) ear length, L, in the S_2 progeny trials

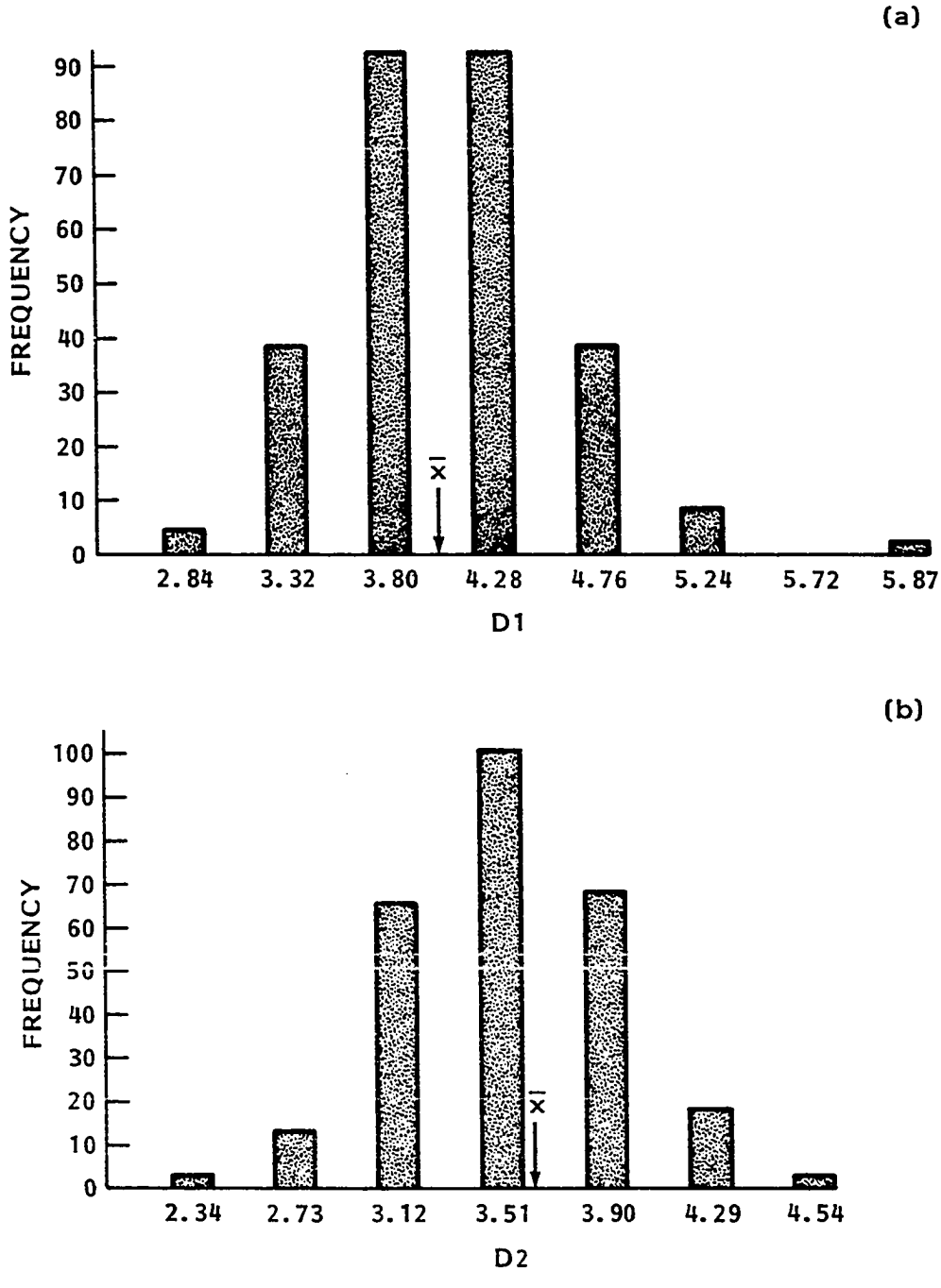

Figure 20. Distribution of the alternate ear diameters, (a) D_1 and (b) D_2, in the S_2 progeny trials

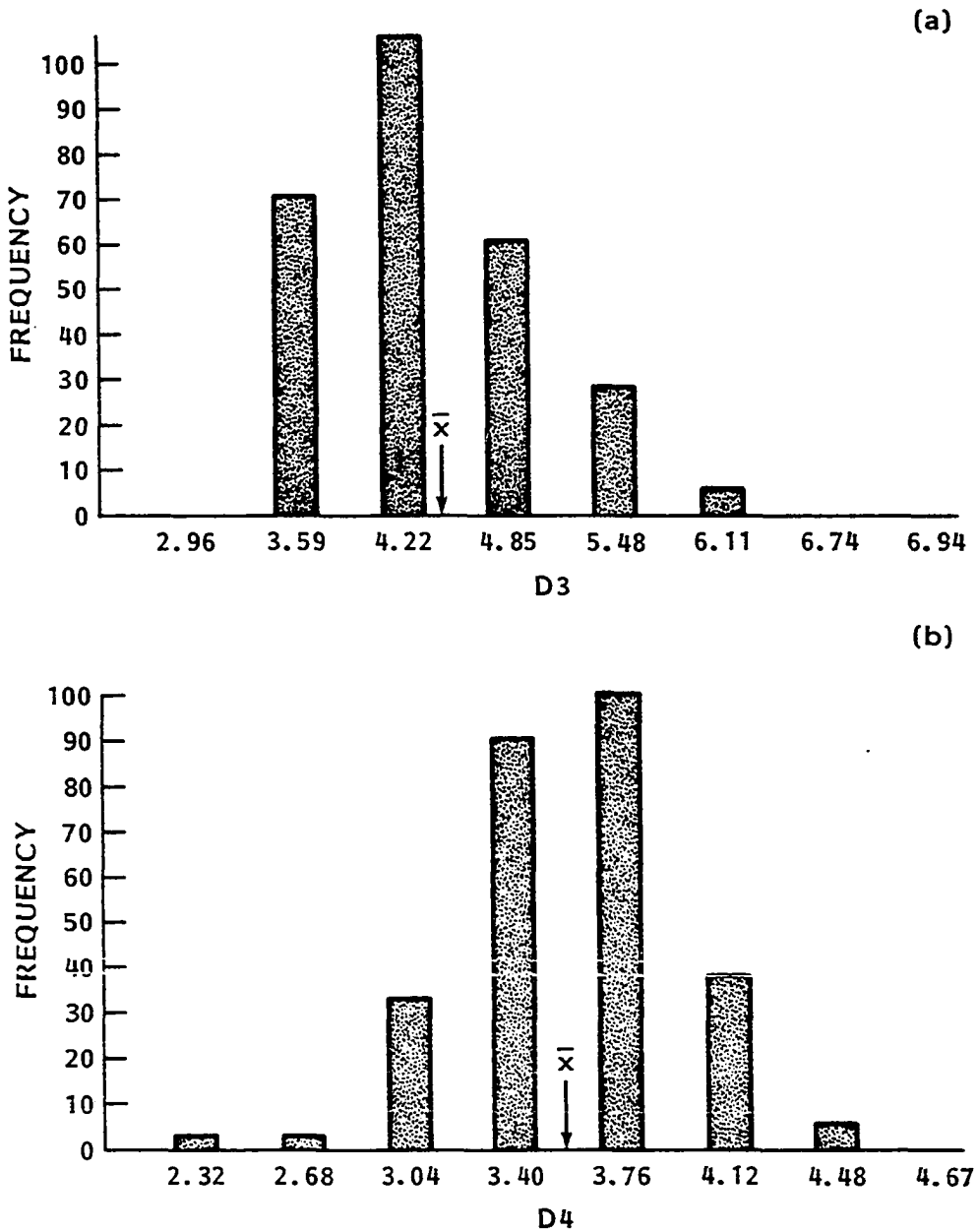

Figure 21. Distribution of the alternate ear diameters (a) D_3 and (b) D_4 in the S_2 progeny trials

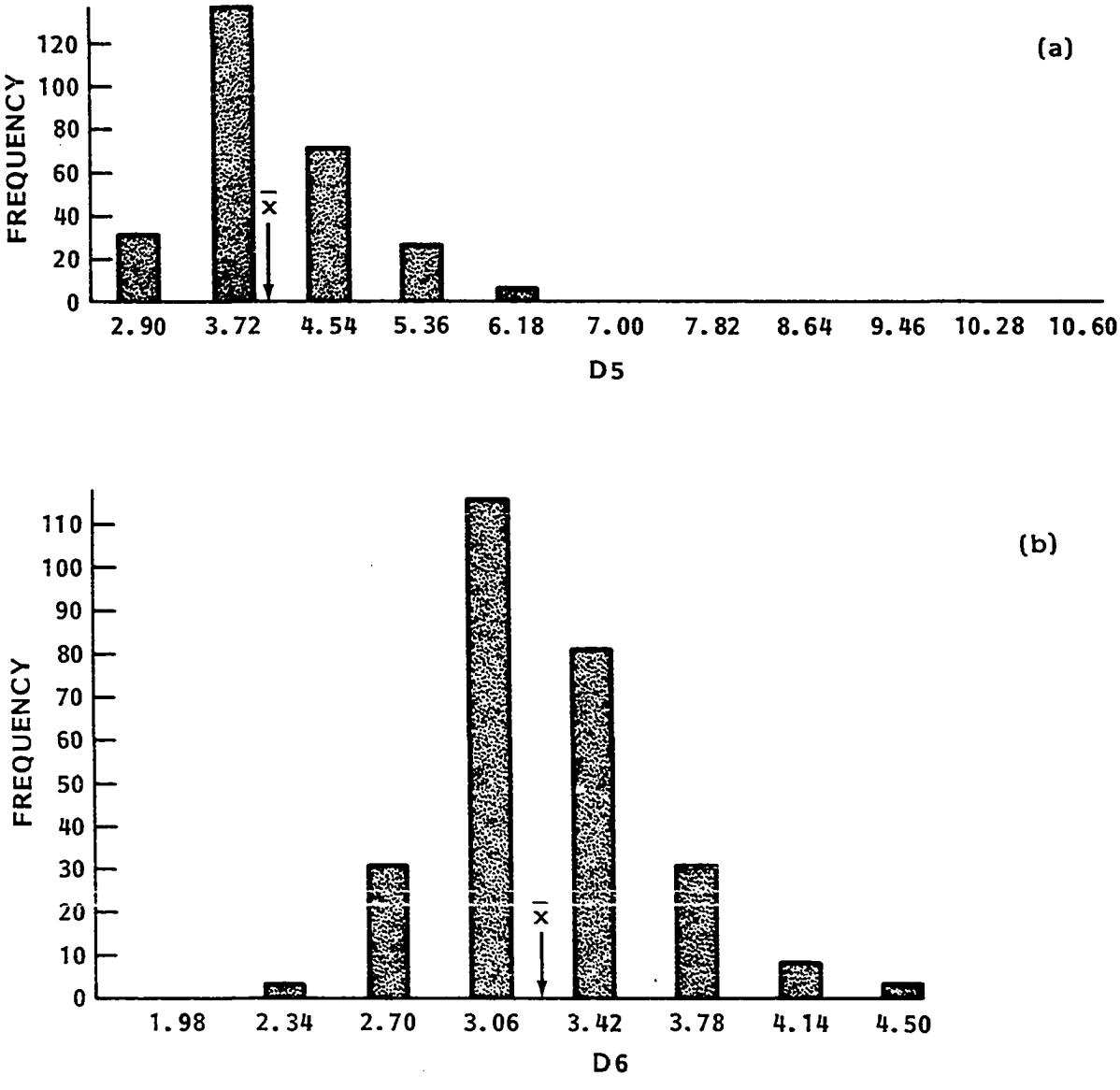

Figure 22. Distribution of the alternate ear diameters (a) D_5 and (b) D_6 in the S_2 progeny trials

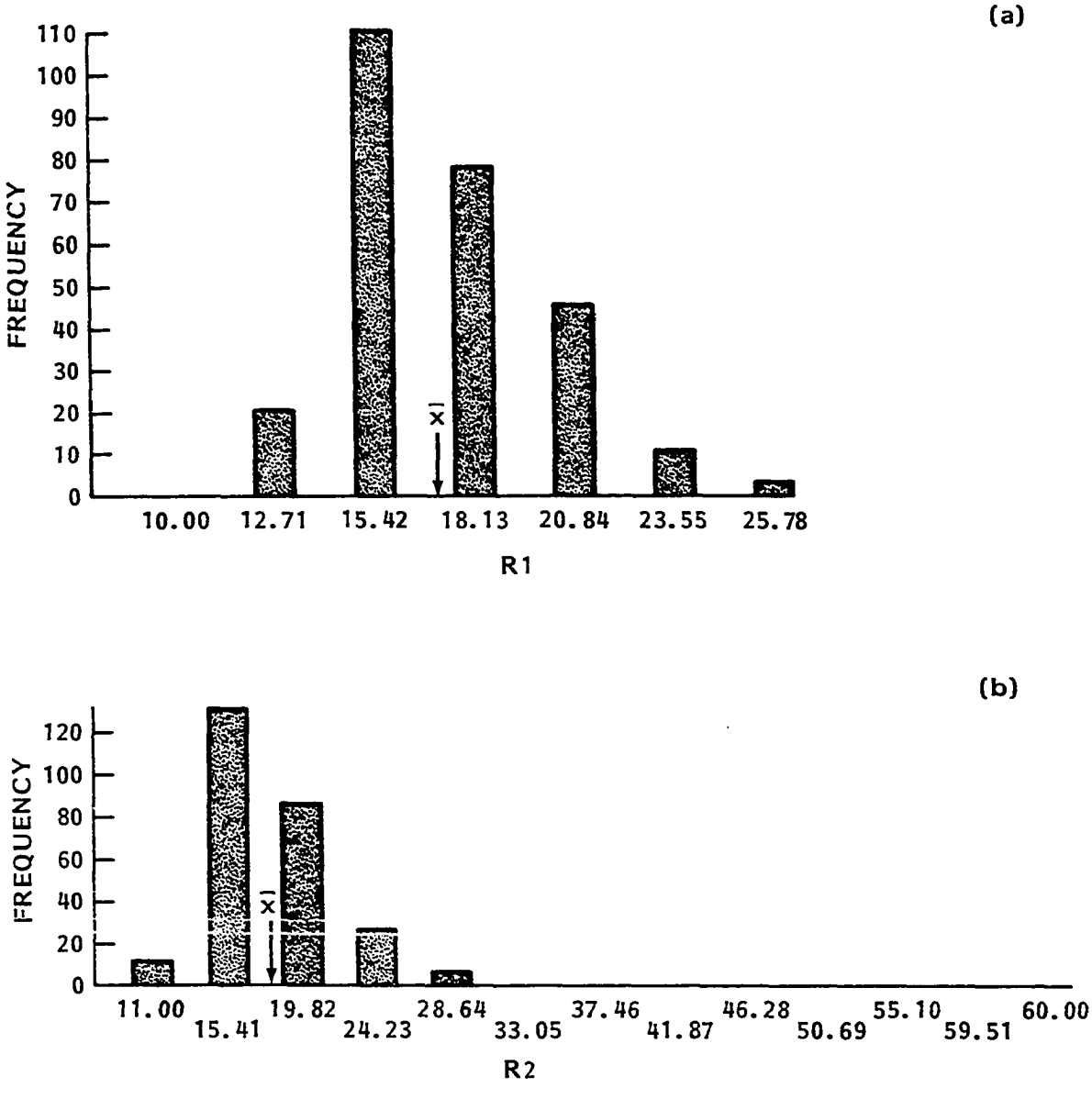

Figure 23. Distribution of kernel-row numbers (a) R_1 and (b) R_2 in the S_2 progeny trials

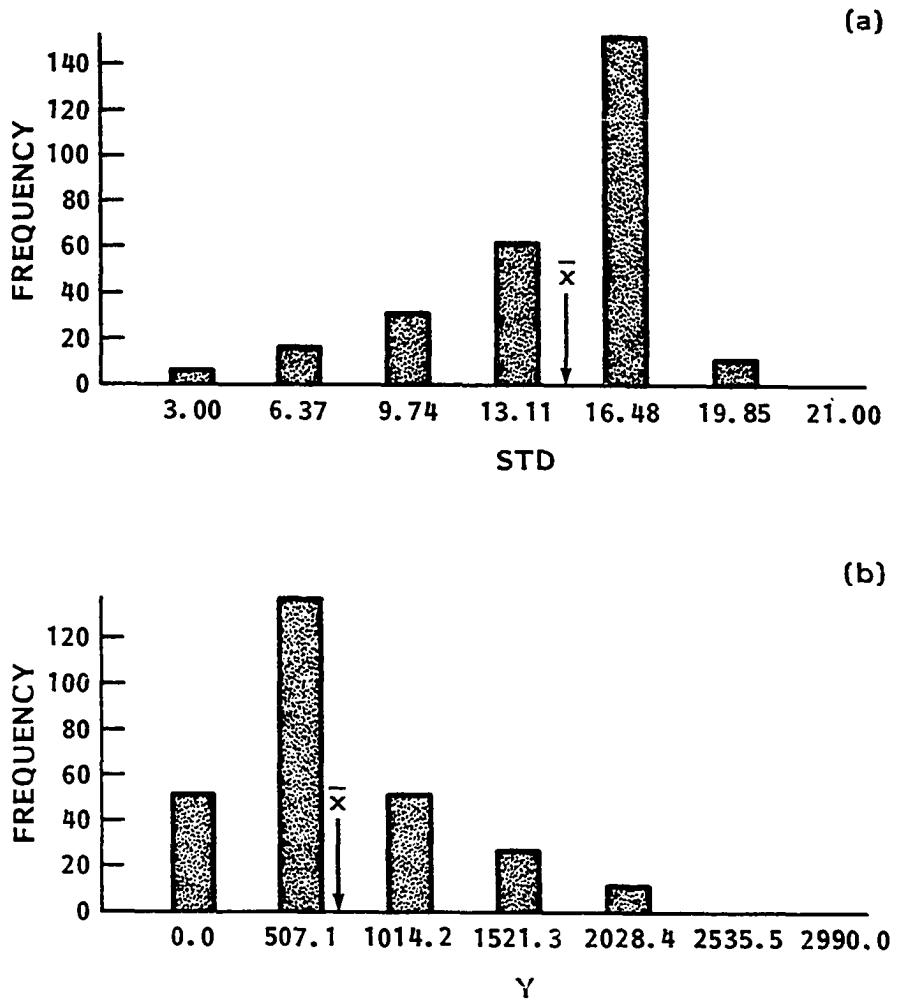

Figure 24. Distribution of (a) stand count, STD, and (b) yield, Y, in the S_2 progeny trials

diameters (D_1 and D_2). The pattern distribution for D1 (Figure 20a) has a slight skewness to the left, which is identical to the same character distribution in the S_1 progenies (Figure 14a). The ear diameter D_2, however, had a nearly normal distribution, suggesting that this trait was more stable in the S_2 than in the S_1 progenies (Figure 14b).

Figure 21 includes the middle pair of alternate diameters, D_3 and D_4. A similar comparison, shown for D_1 and D_2, can be made between the S_1 and S_2 progenies. For both S_1 and S_2 progenies, the diameter D_3 presents a skewness to the left (Figures 15a and 21a), but it was more pronounced in the S_2 progenies. The diameter D_4 showed a distribution closer to the normal distribution in the S_2 progenies (Figure 21b) than in the S_1 progenies (Figure 15b).

The distribution patterns of the D_5 and D_6 alternate diameters (Figure 22) are almost identical to those shown for the S_1 progenies for the same trait (Figure 16): pronounced skewness to the left, suggesting partial dominance involved for D_5 (Figure 22a), and a slight skewness to the left for D_6 (Figure 22b). In the D_6 diameter, the distribution differs a little from that same trait in the S_1 progenies (Figure 16b).

Distributions for the two kernel-row number counts are shown in Figure 23. For the R_1 parameter (Figure 23a), the

distribution shows a pronounced skewness to the left, suggesting partial dominance favoring the lower kernel-row number. This is a different situation from that presented in Figure 17a for the same trait in the S_1 progenies. But for trait R_2, the distributions in both S_1 (Figure 17b) and S_2 progenies (Figure 23b) were similar. There was a pronounced skewness to the left for R_2, for lower number of kernel rows. The range of values for the R_2 trait should be noted because the maximum kernel-row number count in my study was 60 rows.

Figure 24 represents the distribution patterns for stand count (STD) and yield (Y). Strong skewness in opposite directions was obtained: stand was skewed to the right (Figure 24a) and yield was skewed to the left (Figure 24b). This represents a similar situation to that found for the same traits in the S_1 progenies (Figures 18a and 18b). The skewness observed for stand and yield of the S_1 and S_2 progenies reflect type of progenies evaluated and experimental procedures. Plots were overplanted and thinned to insure better stands. Because yield is the trait of greatest economic importance, these findings suggest that yield for the PRV 30 S_2 progenies (as well as for the S_1 progenies) was affected by partial dominance effects. Inbreeding tended to reduce yield expression with a greater frequency of progenies occurring in the lower yielding

classes.

Table 22 includes the phenotypic and genotypic correlation coefficients between all traits (except STD) in the S_2 progenies. It should be emphasized, however, that the genotypic correlation coefficients were expected to be biased by environmental effects, because the S_2 progeny trials were grown in only one environment. Data in Table 22 show, however, that the phenotypic and genotypic correlation coefficients were very similar. From Table 22, we can conclude the following for the relation between the different traits:

1. Fasciation expression (FA) was negatively correlated with all traits, except ear length (r=0.09) and yield (r=0.06). This series of correlations between traits shows that the greater the fasciation rating (lower values), the greater the other traits, except for ear length and yield.
2. Ear diameters D_1, D_3 and D_5 and kernel-row numbers R_1 and R_2 showed: (a) no significant correlation with ear length (L) and yield (Y); (b) significantly negative correlations with fasciation expression (FA); and (c) significantly positive correlations between the pairs of diameter measurements and kernel-row counts.
3. Ear diameter D_2 showed: (a) significant negative correlation (r=-0.25*) with fasciation expression

Table 22. Phenotypic and genotypic (in parentheses) correlation coefficients between traits for 90 S_2 progenies

	Traits[a]				
Traits	D_1	D_3	D_5	D_2	D_4
FA	-0.55** (-0.57)	-0.75** (-0.75)	-0.77** (-0.79)	-0.25* (-0.25)	-0.33** (-0.33)
D_1		0.86** (0.87)	0.75** (0.78)	0.89** (0.90)	0.80** (0.81)
D_3			0.95** (0.98)	0.67** (0.68)	0.81** (0.81)
D_5				0.53** (0.54)	0.71** (0.74)
D_2					0.85** (0.86)
D_4					
D_6					
R_1					
R_2					
L					

[a]Designations are FA - fasciation expression, D_1, D_3, D_5, D_2, D_4, D_6 - ear diameters, R_1 and R_2 - kernel-row number, L - ear length, and Y - yield.

*,**Indicate significance at the 5 and 1% probability levels, respectively.

Traits				
D_6	R_1	R_2	L	Y
-0.40** (-0.40)	-0.66* (-0.67)	-0.71** (-0.75)	0.09 (0.10)	0.06 (0.06)
0.72** (0.73)	0.79** (0.82)	0.63** (0.66)	0.09 (0.06)	0.06 (0.06)
0.82** (0.83)	0.85** (0.87)	0.85** (0.88)	0.05 (0.03)	0.08 (0.08)
0.80** (0.82)	0.79** (0.83)	0.93** (0.93)	0.08 (0.05)	0.04 (0.04)
0.71** (0.72)	0.67** (0.69)	0.43** (0.44)	0.22* (0.20)	0.18 (0.18)
0.93** (0.95)	0.74** (0.75)	0.65** (0.68)	0.19 (0.18)	0.23* (0.23)
	0.70** (0.71)	0.75** (0.78)	0.22* (0.20)	0.15 (0.16)
		0.85** (0.90)	-0.06 (-0.08)	0.14 (0.15)
			0.00 (-0.03)	0.06 (0.07)
				0.56** (0.57)

(FA); (b) no correlation with yield (Y); (c) significantly positive correlation with ear length (r=0.22*); and (d) significantly positive correlations with the remaining traits ($P \leq 0.01$).

4. Ear diameter D_4 showed: (a) significantly negative correlation with fasciation expression (r=-0.33**); (b) no significant correlation with ear length; (c) significantly positive correlation with yield (r=0.23*); and (d) significantly positive correlations with the remaining traits (D_1, D_3, D_5, D_2, D_6, R_1, and R_2).
5. Ear diameter D_6 showed: (a) significantly negative correlation with fasciation expression (r=-0.40**): (b) no significant correlation with yield (Y); (c) significantly positive ($P \leq 0.05$) correlation with ear length (r=0.22*); and (d) significantly positive ($P \leq 0.01$) correlations with the remaining traits.
6. Kernel-row numbers R_1 and R_2 showed: (a) significantly negative correlations with fasciation expression (r=-0.66** for FA and R_1 and r=-0.71** for FA and R_2); (b) no significant correlations with ear length (L) and yield (Y); and (c) significantly positive correlations with all the other traits (D_1, D_3, D_5, D_2, D_4, and D_6). Also, there

was a highly positive correlation between the two kernel-row counts (r=0.85** for R_1 and R_2).

7. Correlation coefficients for ear length (L) showed: (a) significant, but low, positive correlation with D_6 (r=0.22*) and D_2 (r=0.22*); (b) highly significant correlation with yield (r=0.56**); and (c) no significant correlation with D_1, D_3, D_5, D_4, R_1, and R_2.

Data presented in Table 22 suggested that for the S_2 progenies the set of 11 variables measured and their relative importance to yield could probably be reduced to two (L and D_4), for the following reasons: (a) ear length (L) was the only parameter positively correlated with yield (r= 0.56**); and (b) among the six ear diameters, D_4 seemed to be the most important due to the significantly positive correlation of D_4 with yield (r=0.23*).

Table 23 shows the data for the multiple regression analysis of the S_2 progenies for the different traits regressed on yield. Results of the multiple regression analysis are listed in Table 23 by fitting sequentially regression models that included more traits. The best regression model explained only 63.2% of the total sum of squares for yield; 59.5% out of 63.2% was explained by a multiple regression model that included only four parameters (L, STD, R_1, and D_5). The results of the multiple regression

Table 23. Multiple regression analysis of the S_2 progenies for the different traits regressed on yield

Source (regression model)	df	Sum of squares
L/Y	1	5241892.74
STD/Y	1	4681648.30
L STD/Y	2	9923541.04
R_1/Y	1	466822.38
L STD R_1/Y	3	10390363.42
D_5/Y	1	761144.12
L STD R_1 D_5/Y	4	11151507.54
D_3/Y	1	99460.49
L STD R_1D_5 D_3/Y	5	11250968.03
R_2 replaces R_1		35411.95
L STD R_2 D_5 D_3/Y	5	11286379.98
D_6/Y	1	68613.53
L STD R_2 D_5 D_3 D_6/Y	6	11354993.51
D_4 replaces D_3		23146.92
L STD R_2 D_5 D_4 D_6/Y	6	11378140.43
R_1 replaces R_2		32783.21
L STD R_1 D_5 D_4 D_6/Y	6	11410923.64
D_1 replaces D_5		341287.68

[a]Trait designations are: FA - fasciation expression, D_1, D_3, D_5, D_2, D_4, D_6 - ear diameters, R_1 and R_2 - kernel-row numbers, L - ear length, STD - stand count, and Y - yield.

Variables included in models[a]	R-square, %
L if alone	(28.0)
STD if after L	(24.9)
	52.9
R_1 if after L STD	(2.5)
	55.4
D_5 if after L STD R_1	(4.1)
	59.5
D_3 if after L STD R_1 D_5	(0.5)
	60.0
R_2 if after L STD and before D_5 D_3	(0.2)
	60.2
D_6 if after L STD R_2 D_5 D_3	(0.4)
	60.6
D_4 if after L STD R_2 D_5 and before D_6	(0.1)
	60.7
R_1 if after L STD and before D_5 D_4 D_6	(0.2)
	60.9
D_1 if after L STD R_1 and before D_4 D_6	(1.8)

Table 23. (Continued)

Source (regression model)	df	Sum of squares
L STD R_1 D_1 D_4 D_6/Y	6	11752211.32
D_2/Y		17723.19
L STD R_1 D_1 D_4 D_6 D_2/Y	7	11769934.51
D_5 replaces D_1		2827.55
L STD R_1 D_5 D_4 D_6 D_2/Y	7	11772762.06
D_1/Y	1	31035.96
LSTD R_1 D_5 D_4 D_6 D_2 D_1/Y	8	11803798.02
D_3 replaces D_2		24944.01
L STD R_1 D_5 D_4 D_6 D_3 D_1/Y	8	11828742.23
D_2/Y	1	16287.43
L STD R_1 D_5 D_4 D_6 D_3 D_1 D_2/Y	9	11845029.66
FA/Y	1	1948.14
L STD R_1 D_5 D_4 D_6 D_3 D_1 D_2 FA/Y	10	11846977.80
R_2/Y	1	2038.25
L STD R_1 D_5 D_4 D_6 D_3 D_1 D_2 FA R_2/Y	11	11849016.05
Error	76	6900237.18
Total	87	18749253.23

Variables included in models	R-square, %
	62.7
D_2 if after L STD R_1 D_1 D_4 D_6	(0.1)
	62.8
D_5 if after L STD R_1 and before D_4 D_6 D_2	(0.0)
	62.8
D_1 if after L STD R_1 D_5 D_4 D_6 D_2	(0.2)
	63.0
D_3 if after L STD R_1 D_5 D_4 D_6 and before D_1	(0.1)
	63.1
D_2 if after L STD R_1 D_5 D_4 D_6 D_3 D_1	(0.1)
	63.2
FA if after L STD R_1 D_5 D_4 D_6 D_3 D_1 D_2	(0.0)
	63.2
R_2 if after L STD R_1 D_5 D_4 D_6 D_3 D_1 D_2 FA	(0.0)
	63.2
	36.8
	100.0

analysis can be used to partially correct our previous conclusions based on the correlations among traits (Table 22). According to the correlation (Table 22) and regression analyses, ear diameter D_5 was more important than D_4 for determining yield. This suggests that a model that includes ear length (L), stand count (STD), kernel-row number R_1, and ear diameter D_5 would be the best four-parameter regression model to explain yield (Y) in the S_2 progenies.

3. Diallel

The diallel trial assumes a particular importance in my studies because it was based on a set of eight original parents representing not only the PRV 30, but also five more PRVs and two inbreds having fasciation expression. Consequently, the results have to be considered as representing a wider range of fasciated germplasm than that of PRV 30, which formed the basis of my previous studies. Table 24 includes data of the analysis of variance for a set of eight parents, their diallel crosses and 14 checks (for pedigrees see Table 27). The traits evaluated are the same previously studied for S_1 and S_2 progenies. The diallel analysis of variance (Table 24) shows:

1. For entries and diallel (entries 1 to 35 in Table 27) sources of variation, there were highly significant differences ($P \leq 0.01$) for all traits.
2. For parents (entries 1 to 8 in Table 27), there were

Table 24. Analysis of variance for the 8 parents, 28 diallel crosses and 12 checks for fasciation expression (FA), ear diameters (D_1 to D_6), kernel-row numbers (R_1 and R_2), ear length (L), stand count (STD), and yield (Y)

Source of variation	df	Mean squares				
		FA	D_1	D_3	D_5	D_2
Rep	2	0.05	0.04	0.03	0.09	0.03
Entries	49	9.88**	0.59**	1.22**	1.47**	0.31**
Diallel	35	4.11**	0.70**	1.39**	1.63**	0.37**
Parents	7	6.16**	0.44**	1.46**	1.81**	0.10**
Parents vs crosses	1	8.17**	10.51**	9.41**	10.91**	8.48**
Crosses	27	3.43**	0.40**	1.07**	1.25**	0.14**
GCA	7	11.00**	1.34**	3.53**	4.18**	0.30**
SCA	20	0.78**	0.07**	0.21**	0.22**	0.08**
Diallel vs checks	1	188.36**	1.07**	7.16**	8.39**	0.55**
Checks	13	11.70**	0.25**	0.30**	0.51**	0.14**
A632 testcrosses	6	2.32**	0.12**	0.11**	0.15**	0.12**
A632 test. vs Rest	1	36.14**	1.44**	2.18**	3.58**	0.46**
Rest	6	17.01**	0.18**	0.19**	0.35**	0.10**
Hybrids	3	8.76**	0.15**	0.17**	0.20**	0.06*
Portuguese hyb.	2	11.00**	0.04	0.02	0.13*	0.01
Port. hyb. vs (A632xA619)	1	4.28**	0.37**	0.49**	0.36**	0.16**
ralral testcrosses	2	7.78**	0.14**	0.16**	0.33**	0.11**
Hyb. vs ralral testcrosses	1	60.22**	0.37**	0.27**	0.84**	0.22**
Error	98	0.17	0.02	0.02	0.03	0.02
Total	149					
GCA effects/SCA effects		8.25	12.75	8.56	10.06	2.20
Means		5.63	5.05	5.08	4.70	4.52
CV (%)		7.25	2.64	2.64	3.78	2.79

*,**Indicate significance at the 5 and 1% probability levels, respectively.

Mean squares						
D_4	D_6	R_1	R_2	L	STD	Y
0.01	0.01	1.93**	1.75	1.05	4.09	882105.17
0.29**	0.25**	17.34**	32.10**	27.81**	47.69**	8953458.16**
0.33**	0.27**	15.79**	32.23**	14.42**	58.89**	7465422.56**
0.19**	0.15**	21.06**	53.78**	1.27**	192.52**	853100.00
6.32**	5.05**	116.47**	129.11**	252.28**	518.00**	155617000.59**
0.14**	0.13**	10.70**	23.06**	9.01**	7.24	3692632.93**
0.42**	0.42**	35.16**	77.01**	28.10**	11.84	12516242.76**
0.04**	0.03**	2.13**	4.18**	2.34**	5.63	604369.48
0.06*	0.17**	154.36**	294.84**	747.59**	76.19**	122827150.30**
0.21**	0.21**	10.97**	11.54**	8.50**	15.36**	4200193.09**
0.07**	0.06**	3.77**	3.38**	1.54**	16.21*	3235990.08**
0.45**	0.44**	32.23**	40.11**	0.38	1.92	2968029.16*
0.32**	0.33**	14.62**	14.93**	16.82**	16.75*	5369756.75**
0.11**	0.08**	20.50**	20.33**	22.58**	14.75	388757.64
0.00	0.03	14.71**	14.62**	30.21**	19.00	148358.34
0.32**	0.18**	32.09**	31.74**	7.32**	6.25	869556.25
0.00	0.01	4.48**	7.63**	0.70	2.78	5702258.34**
1.58**	1.70**	17.25**	13.35**	31.76**	50.67**	19647750.89**
0.01	0.01	0.39	0.65	0.43	6.30	462949.21
5.33	8.00	9.33	10.11	6.04	-	1.51
4.39	3.92	19.32	19.71	14.40	31.83	3921.67
2.16	3.06	3.23	4.08	4.57	7.89	17.35

highly significant differences for all traits, except for yield, which was not significantly different from zero.

3. The comparison between parents and crosses (entries 9 to 36 in Table 27) gave highly significant differences for all traits.
4. There were highly significant differences for crosses and general combining ability (GCA) for all traits, except for stand count (STD).
5. Specific combining ability (SCA) was not significant for yield and stand count, and highly significant for all the other traits.
6. The comparison between diallel and checks (entries 37 to 50 in Table 27) showed significant differences for ear diameter D_4 and highly significant differences for all the other traits.
7. Variation among checks was highly significant for all traits.
8. Testcrosses with the inbred A632 (entries 37 to 43 in Table 27) showed significant differences ($P \leq 0.05$) for STD and highly significant differences ($P \leq 0.01$) for all the remaining traits.
9. The comparison between A632 testcrosses and rest (entries 44 to 50 in Table 27) was not significant for ear length and stand count; there were signifi-

cant differences ($P \leq 0.05$) for yield, and highly significant differences for all the other traits.

10. The component "rest" showed significant differences for STD, and highly significant differences for the remaining traits.
11. Variance among hybrids (entries 44 to 46, and entry 50 in Table 27) showed no significant differences for Y and STD, a significant difference ($P \leq 0.05$) for D_2, and highly significant differences for all the other traits.
12. Variation among Portuguese hybrids (entries 44 to 46 in Table 27) was not significantly different from zero for the following traits: ear diameters D_1, D_3, D_2, D_4, and D_6, as well as for stand and yield. A significant difference ($P \leq 0.05$) was found for ear diameter D_5, and highly significant differences for fasciation expression, kernel-row numbers R_1 and R_2, and for ear length.
13. The comparison between Portuguese hybrids and the single cross, A632 x A619 (entry 50 in Table 27), showed highly significant differences for all traits, except stand and yield.
14. Testcrosses with the homozygous ramosa 1 source (ra1ra1) showed no significant differences for ear diameters D_4 and D_6, ear length, and stand count.

But the differences were highly significant for all the other traits.

15. There were highly significant differences for all traits between hybrids and ralral testcrosses.

Table 24 also includes coefficients of variation (CV) and overall means for each trait, as well as the ratio between GCA effects over SCA effects. GCA and SCA effects were calculated according to Hallauer and Miranda (1981). The magnitude of that ratio indicates that GCA is preponderant over SCA for all traits evaluated; SCAs largest value was for ear diameter D_1 (12.75), and the lowest value was for yield (1.51). It should be emphasized that the parents included in the diallel trial were chosen among the most extreme cases for fasciation expression. Hence, the results obtained for the relative importance of GCA and SCA effects were considered critical information relating to the fasciation character. Because GCA is primarily associated with additive gene action, these findings support our previous conclusions about the recessiveness of fasciation expression and the small importance played by dominance in this Portuguese germplasm.

Table 25 presents the phenotypic correlation coefficients for the diallel crosses (entries 8 to 36 in Table 27). From Table 25 we have:

1. Fasciation expression was negatively correlated with ear diameters D_1 (r=-0.73**), D_3 (-0.85**),

Table 25. Phenotypic correlation coefficients between traits for the diallel crosses

Traits	Traits				
	FA	D_1	D_3	D_5	D_2
FA		-0.73**	-0.85**	-0.86**	-0.06
D_1			0.90**	0.82**	0.50**
D_3				0.96**	0.20
D_5					0.20
D_2					
D_4					
D_6					
R_1					
R_2					
L					

*,**Indicate significance at the 5% and 1% probability levels, respectively.

Table 26. Phenotypic correlation coefficients between the parents means and the respective crosses means, in the diallel crosses

Traits	Traits				
	FA	D_1	D_3	D_5	D_2
FA	0.75**				
D_1		0.83**			
D_3			0.88**		
D_5				0.90**	
D_2					0.40**
D_4					
D_6					
R_1					
R_2					
L					
Y					

*,**Indicate significance at the 5% and 1% probability levels, respectively.

Traits					
D_4	D_6	R_1	R_2	L	Y
-0.14	-0.03	-0.65**	-0.80**	0.53**	0.34
0.39*	0.26	0.74**	0.71**	-0.35	-0.23
0.30	0.19	0.79**	0.87**	-0.52**	-0.32
0.29	0.22	0.78**	0.92**	-0.38*	-0.16
0.74**	0.71**	0.42*	0.24	0.30	0.47*
	0.96**	0.65**	0.46*	-0.02	0.38*
		0.57**	0.40*	0.18	0.55**
			0.91**	-0.30	0.08
				-0.31	0.02
					0.84**

Traits					
D_4	D_6	R_1	R_2	L	Y
0.75**					
	0.76**				
		0.85**			
			0.89**		
				0.36	
					0.71**

and D_5 (r=-0.86**), and with kernel-row numbers R_1 (r=-0.65**) and R_2 (r=-0.80**). But fasciation expression was positively correlated with ear length (r=0.53**).

2. Ear diameters D_1, D_3, and D_5 showed a negative correlation with fasciation expression and a positive correlation with all other traits except L and Y.
3. Ear diameter D_2 was correlated with D_1 (r=0.50**), D_4 (r=0.74**), D_6 (r=0.71**), R_1 (r=0.42*), and yield (r=0.47*).
4. Ear diameter D_4 was correlated with D_1 (r=0.39*), D_2 (r=0.74**), D_6 (r=0.96**), R_1 (r=0.65**), R_2 (r=0.46*), and yield (r=0.38*).
5. Ear diameter D_6 was correlated with D_2, D_4, R_1 (r=0.57**), R_2 (r=0.40*), and yield (r=0.55**).
6. Kernel-row number R_1 was negatively correlated with fasciation expression (r=-0.65**), and positively correlated with all the other traits, except ear length and yield.
7. Kernel-row number R_2 was also negatively correlated with fasciation expression, had no significant correlation with ear length and yield, and was positively correlated with the remaining traits.
8. Ear length had a significantly negative correlation with D_3 (r=-0.52**) and D_5 (r=-0.38*), and signifi-

cant positive correlations with FA (r=0.53**) and Y (0.84**).

The correlation coefficients shown in Table 25 suggest that for the diallel crosses the 11 parameters measured could be reduced to only diameter D_6 and ear length (L), for the following reasons: (a) ear diameter D_6 was highly correlated with yield (r=0.55**) and had no significant correlation with fasciation expression (r=-0.03), and (b) ear length (L) had the greatest correlation with yield (r=0.84**).

Table 26 includes the phenotypic correlation coefficients between the parents mean values and the respective single-crosses means in the diallel crosses. Table 26 shows that there were significant correlations for all traits, except for ear length. This suggests that the trait ear length (L) was a complex trait, as results included in Table 27 seem to suggest.

Table 27 includes the means and pedigrees of the diallel entries for the 12 traits: FA, D_1, D_3, D_5, D_2, D_4, D_6, R_1, R_2, L, STD, and Y. The eight parents included six PRV-S_1s and two inbreds (entries 7 and 8 in Table 27), which are the parents of the female single-cross of the Portuguese double-cross hybrid HB19. Both inbreds (WF9R and 38-11/2) have the fasciation expression in a controlled way; that is, in a moderate level of expression. Results from Table 27 show:

Table 27. Means and pedigrees of the 8 parents, 28 diallel crosses, and 14 checks, for fasciation expression (FA), ear diameters (D_1 to D_6), kernel-row numbers (R_1 and R_2), ear length (L), stand count (STD), and yield (Y)

Entry no.	Pedigree	Traits			
		FA[a]	D_1	D_3	D_5
		cm			
1	PRV 30-56	2.9	4.99	6.11	5.99
2	PRV 37-13	5.5	4.67	4.86	4.28
3	PRV 38-61	4.4	4.89	5.11	4.67
4	PRV 99-15	5.2	4.66	4.48	3.96
5	PRV 214-18	5.9	4.41	4.44	3.93
6	PRV 216-9	6.7	4.52	4.28	3.83
7	38-11/2-19	5.5	3.86	3.87	3.58
8	WF9-R	7.6	4.11	4.20	3.79
	Parents $\bar{X}$	5.5	4.51	4.67	4.25
9	PRV 30-56 x PRV 37-13	3.3	5.74	6.41	5.97
10	PRV 30-56 x PRV 38-61	3.4	5.68	6.47	6.56
11	PRV 30-56 x PRV 99-15	3.2	5.87	6.54	6.37
12	PRV 30-56 x PRV 214-18	3.8	5.48	6.02	5.67
13	PRV 30-56 x PRV 216-9	3.4	5.68	6.34	6.12
14	PRV 30-56 x 38-11/2-19	4.4	5.00	4.81	4.88
15	PRV 30-56 x WF9-R	4.0	5.68	5.77	5.46
	PRV 30-56 $\bar{X}$	3.6	5.59	6.05	5.86
16	PRV 37-13 x PRV 38-61	4.2	5.39	5.54	5.00
17	PRV 37-13 x PRV 99-15	4.3	5.55	5.56	5.03
18	PRV 37-13 x PRV 214-18	4.9	5.13	5.40	4.85
19	PRV 37-13 x PRV 216-9	4.5	5.56	5.59	5.17
20	PRV 37-13 x 38-11/2-19	5.6	4.87	4.93	4.42
21	PRV 37-13 x WF9-R	5.8	5.57	5.39	4.82
	PRV 37-13 $\bar{X}$	4.7	5.40	5.55	5.04
22	PRV 38-61 x PRV 99-15	3.4	5.48	5.88	5.34
23	PRV 38-61 x PRV 214-18	4.2	5.46	5.49	4.98
24	PRV 38-61 x PRV 216-9	3.7	5.47	5.79	5.55
25	PRV 38-61 x 38-11/2-19	4.4	4.87	4.89	4.75
26	PRV 38-61 x WF9-R	4.9	5.37	5.28	4.93
	PRV 38-61 $\bar{X}$	4.0	5.39	5.62	5.30

[a]Visual rating from 1 (ralral expression) to 9 (normal type.

Traits							
D_2	D_4	D_6	R_1	R_2	L	STD	Y
--------cm--------			------no.-----		cm	no.	g/plot
4.09	4.29	3.77	23.68	28.10	9.90	32.00	1418.33
4.08	4.11	3.65	18.51	18.48	9.50	29.33	626.67
4.17	4.04	3.61	19.20	19.91	10.94	33.67	1508.33
3.78	3.52	3.16	15.46	15.23	10.07	30.67	690.00
3.83	3.90	3.44	16.83	16.53	9.44	12.00	348.33
4.10	3.77	3.24	15.52	14.74	10.83	28.33	1345.00
3.66	3.68	3.38	16.88	16.85	10.90	18.00	1020.00
3.97	4.05	3.67	18.00	18.47	9.60	34.33	1936.67
3.96	3.92	3.49	18.01	18.54	10.15	27.29	1111.67
4.62	4.77	4.20	23.52	26.11	12.13	30.33	3313.33
4.63	4.62	4.13	23.42	27.13	12.69	32.67	3756.67
4.64	4.34	3.88	22.70	25.72	14.00	34.33	3613.33
4.52	4.64	4.11	23.31	24.11	11.18	32.33	3823.33
4.63	4.56	4.05	22.07	25.35	12.69	33.33	3726.67
4.72	4.36	3.91	20.31	21.73	16.58	33.67	5536.67
5.11	5.01	4.49	23.69	24.34	14.66	32.33	5573.33
4.70	4.61	4.11	22.72	24.93	13.42	32.71	4191.90
4.52	4.53	4.06	20.55	21.45	12.33	33.00	2920.00
4.62	4.31	3.78	20.02	19.86	12.78	31.00	2306.67
4.43	4.45	3.87	20.29	20.03	10.56	31.00	2305.00
4.81	4.52	4.00	20.09	20.27	12.85	34.33	3345.00
4.54	4.55	3.96	21.46	21.28	13.09	33.33	4291.67
5.17	4.99	4.38	22.00	21.19	13.05	32.33	4121.67
4.53	4.59	4.04	21.13	21.46	12.40	32.19	3229.05
4.38	4.22	3.71	21.77	22.75	12.68	32.67	3291.67
4.69	4.56	3.98	20.55	20.97	13.57	31.00	3280.00
4.67	4.42	3.93	20.33	22.98	13.50	32.67	3950.00
4.65	4.56	4.10	19.09	20.64	15.21	34.00	5375.00
4.90	4.71	4.25	21.62	21.05	15.74	33.67	5558.33
4.63	4.52	4.02	21.05	22.42	13.67	32.81	4018.81

Table 27. (Continued)

Entry no.	Pedigree	Traits FA	D_1	D_3	D_5
27	PRV 99-15 x PRV 214-18	5.3	5.29	5.08	4.48
28	PRV 99-15 x PRV 216-9	5.5	5.27	5.10	4.68
29	PRV 99-15 x 38-11/2-19	6.6	4.72	4.57	4.24
30	PRV 99-15 x WF9-R	7.0	5.06	4.79	4.37
	PRV 99-15 $\bar{X}$	5.0	5.32	5.36	4.93
31	PRV 214-18 x PRV 216-9	5.2	4.80	4.81	4.40
32	PRV 214-18 x 38-11/2-19	5.1	4.61	4.73	4.42
33	PRV 214-18 x WF9-R	5.9	4.83	4.79	4.38
	PRV 214-18 $\bar{X}$	4.9	5.09	5.19	4.74
34	PRV 216-9 x 38-11/2-19	6.2	4.80	4.59	4.29
35	PRV 216-9 x WF9-R	5.2	5.39	5.13	4.77
	PRV 216-9 $\bar{X}$	4.8	5.28	5.34	5.00
36	38-11/2-19 x WF9-R	6.4	4.79	4.85	4.63
	38-11/2-19 $\bar{X}$	5.5	4.81	4.77	4.52
	WF9-8 $\bar{X}$	5.6	5.24	5.14	4.77
37	PRV 30-56 x A632	6.4	4.96	4.76	4.34
38	PRV 37-13 x A632	8.3	4.89	4.58	4.15
39	PRV 38-61 x A632	8.4	4.82	4.61	4.13
40	PRV 214-18 x A632	8.8	4.40	4.22	3.70
41	PRV 216-9 x A632	9.0	4.54	4.28	3.77
42	38-11/2-19 x A632	8.9	4.70	4.51	4.03
43	38-11/2-39 x A632	8.7	4.77	4.58	4.09
	A632 $\bar{X}$	8.4	4.73	4.51	4.03
44	WF9-R x 38-11/2	5.4	4.95	5.03	4.71
45	33-16-R x PB 108	9.0	5.15	4.90	4.32
46	HB19	8.4	5.16	5.01	4.60
47	ral/ral x PRV 30-71	3.2	5.48	5.18	5.10
48	ral/ral x PRV 38-88	4.1	5.22	5.26	4.97
49	ral/ral x PRV 216-101	6.3	5.05	4.83	4.47
50	A619 x A632	9.0	4.68	4.51	4.14

Traits							
D_2	D_4	D_6	R_1	R_2	L	STD	Y
4.62	4.38	3.85	18.45	17.60	13.73	27.00	3056.67
4.66	4.20	3.70	17.43	17.22	14.00	33.00	3078.33
4.44	4.23	3.82	17.84	17.89	16.55	32.33	5010.00
4.60	4.43	4.06	20.14	19.40	17.12	34.33	5290.00
4.57	4.30	3.83	19.76	20.06	14.41	32.09	3663.81
4.25	4.21	3.70	17.60	17.32	11.58	32.00	1858.33
4.32	4.42	3.99	18.79	19.81	12.85	33.33	3463.33
4.48	4.44	4.03	19.95	19.83	14.29	32.00	4145.00
4.47	4.44	3.93	19.85	19.95	12.54	31.24	3133.09
4.49	4.25	3.78	17.26	17.33	15.83	33.00	4978.33
4.96	4.73	4.25	20.74	20.16	15.76	32.00	5348.33
4.64	4.41	3.92	19.36	20.09	13.74	32.90	3755.00
4.66	4.70	4.34	19.19	19.19	16.07	34.67	5655.00
4.55	4.44	3.99	19.13	19.70	15.17	33.48	4901.43
4.84	4.72	4.26	21.05	20.74	15.24	33.05	5098.81
4.65	4.31	3.85	18.77	17.88	18.38	30.00	4936.67
4.63	4.35	3.94	17.22	17.09	17.92	34.67	5565.00
4.56	4.34	3.91	16.58	16.29	18.51	37.33	6628.33
4.13	4.07	3.64	16.15	15.52	16.43	32.00	3800.00
4.37	4.16	3.72	15.17	14.82	18.42	33.33	5493.33
4.62	4.46	3.98	16.50	16.46	17.87	32.00	6406.67
4.65	4.49	4.03	17.32	17.32	17.67	33.00	6640.00
4.52	4.31	3.87	16.82	16.48	17.89	33.19	5638.57
4.82	4.87	4.42	21.04	21.02	15.56	33.33	6351.67
4.90	4.82	4.28	16.63	16.63	21.91	28.33	5930.00
4.91	4.85	4.47	18.52	18.42	18.59	31.33	6018.33
4.82	4.21	3.69	19.99	20.23	16.32	34.00	2458.33
4.45	4.22	3.79	20.60	20.33	16.44	34.00	4380.00
4.54	4.18	3.74	18.25	17.52	17.21	35.67	5131.67
4.61	4.47	4.11	14.95	14.93	20.49	32.67	5478.33

1. For the set of the 28 diallel crosses (entries 9 to 36 in Table 27), significant differences were found among crosses as shown in Table 24. The best yielding crosses for each parent were those which included as the other parent either the WF9-R or 38-11/2 inbreds (entries 14 and 15, 20 and 21, 25 and 26, 29 and 30, 35 and 36 in Table 27).
2. The inbreds, WF9-R and 38-11/2, had the highest mean contribution for yield (5098.81 and 4901.43, respectively, in Table 27), followed by PRV 30-56 (4191.90, Table 27), which was the representative parent of the most extreme case of fasciation expression (see Plate 23). Since PRV 30-56 had a low mean contribution for ear length (13.42, Table 27), its relatively high mean contribution for yield seems to be due to its highest mean contribution for kernel-row number (22.72 and 24.93 for R_1 and R_2, respectively, Table 27).
3. In Table 24, it was shown that there were significant differences among A632 testcrosses and between testcrosses and rest. Among the set of hybrids designated by "rest" was included the single-cross A632 x A619 (entry 50, Table 27), which is a hybrid widely used in the northern range of the U.S. Corn Belt. Three single-crosses (entries 39, 42, and 43

in Table 27) outyielded the single cross A632 x A619 (5478.33) by yields above 6000 g/plot. The best producing single cross (38-11/2 x A632, entry 43 in Table 27) yielded 121.2% (6540.00 g/plot) as compared with A632 x A619. Since all the crosses (except A632 x A619) included fasciated parents, these results indicate that among this type of Portuguese germplasm there was a genetic potential for high yield. These results also indicated that both Portuguese and American germplasm can be advantageously used as an exotic introduction in each country for yield improvement programs.

It should be emphasized, however, that the results shown in Table 27 would be unexpected based on our previous conclusions about the correlations between fasciation (FA) expression and the traits ear length (L) and yield (Y). This unexpected situation can be summarized this way:

1. Ear length (L) has been consistently the most important trait related with yield (Tables 19, 22, and 25).
2. Fasciation expression (FA) has been shown as a trait positively correlated with ear length (Tables 19 and 25); that is, for higher fasciation expression (low rating values) we obtained lower values for ear length. Consequently, we expected a negative in-

fluence of the fasciated germplasm for yield.

To better understand what seemed to be contradictory effects, an attempt was made to study the possible relationship between fasciation and yield. This was made by comparing both traits, fasciation and yield, in the two sets of single crosses: diallel crosses and A632 testcrosses.

Figure 25 shows the regressions of the single-crosses fasciation expression upon the midparent fasciation for both diallel crosses (Figure 25, A) and A632 testcrosses (Figure 25, B). Figure 25 shows: (a) for the diallel crosses, we always obtained in the F_1 generation (single crosses) a type of negative heterosis for fasciation expression and (b) when one of the parents was a nonfasciated type (A632), a positive type of heterosis was obtained for fasciation expression.

Figure 26 shows the regression of yield in the single crosses upon fasciation (midparent values) for both the diallel (Figure 26, A) and A632 testcrosses (Figure 26, B). Although no significant correlation coefficient was obtained, Figure 26 shows a different trend for both sets of crosses. While there is a positive trend for the diallel crosses (b=0.23), a negative trend seems to follow the A632 testcrosses. This suggests that: (a) when both parents are fasciated (diallel crosses), as we have increased fasciation expression (lower values), we should expect lower yield values; and (b) the opposite can happen for A632 testcrosses.

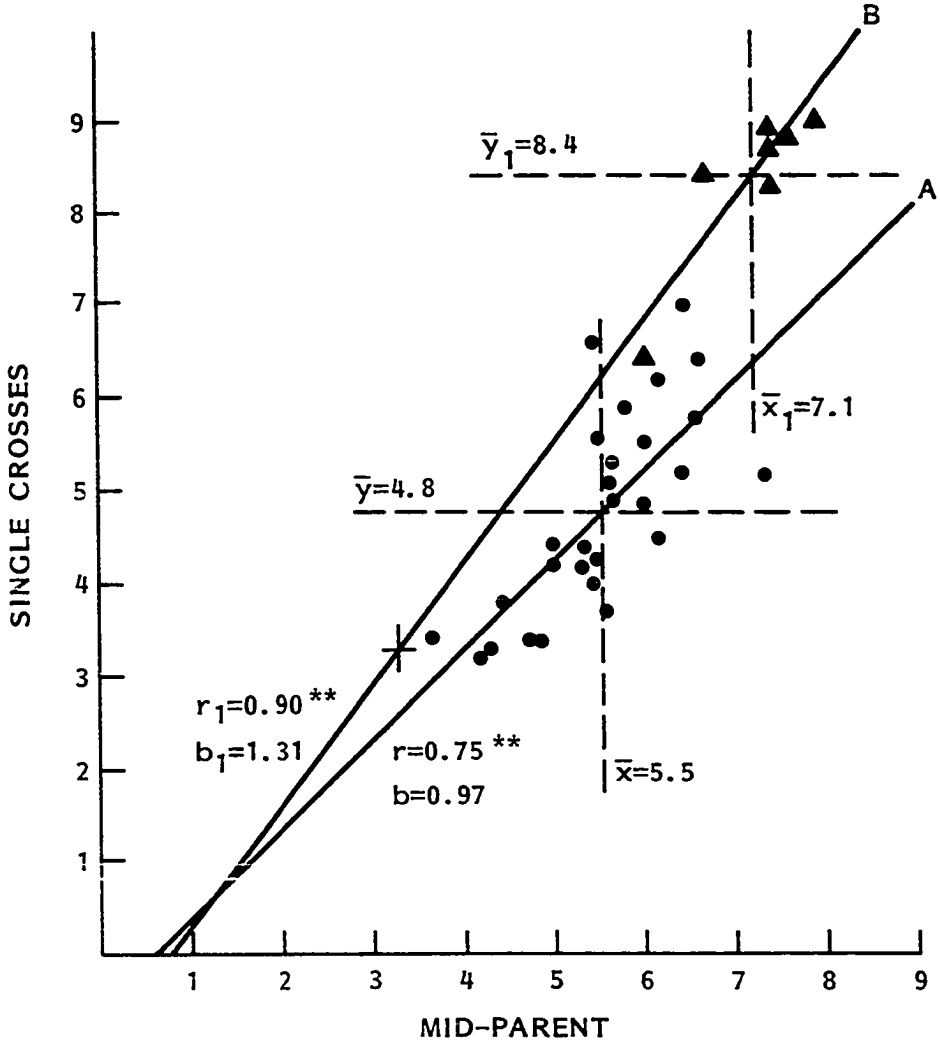

Figure 25. Relationship of fasciation expression between parents and their single crosses in the diallel trial; A - diallel crosses (●) y=-0.57 + 0.97x; B - A632 testcrosses (▲) y_1 = -1.03 + 1.31 x_1

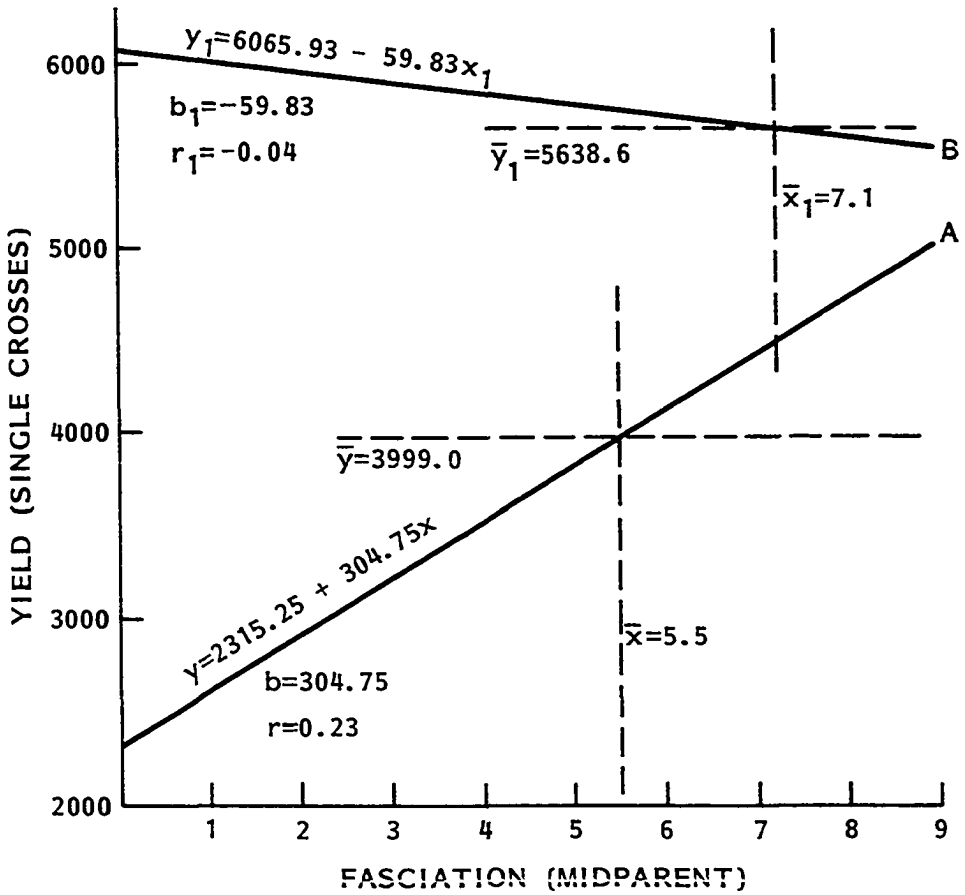

Figure 26. Trends between fasciation expression of the parents (midparent values) and yield of respective single-crosses in the diallel trial; A - diallel crosses; B - A632 testcrosses

Figure 27 relates fasciation expression (midparent values) with ear length in the single crosses, for both the diallel crosses (Figure 27, A) and the A632 testcrosses (Figure 27, B). Figure 27 shows opposite trends for diallel crosses and A632 testcrosses for the relation between fasciation in the parents and ear length in the F_1 generation (single crosses). In other words, Figure 27 shows that, as the inbred A632 was crossed with a stronger fasciated parent, a greater ear length would be obtained in the F_1 generation. But the opposite should be expected when two fasciated parents were crossed, which is similar to our previous conclusions.

Finally, Figure 28 shows the relationship between yield and ear length in the single crosses, for both diallel crosses (Figure 28, A) and A632 testcrosses (Figure 28, B). Figure 28 shows: (a) a significant correlation was obtained for the diallel crosses ($r=0.84^{**}$), as was shown in Table 25; and (b) although there was no significant correlation ($r=0.59$) for the A632 testcrosses, the trend seemed to be even more pronounced than that for the diallel crosses. That is, for the same increase in ear length, a bigger increase in yield was expected for the A632 testcrosses than for the diallel crosses.

Information from Figures 25 to 28 suggests the following inferences: (a) the different heterotic patterns between

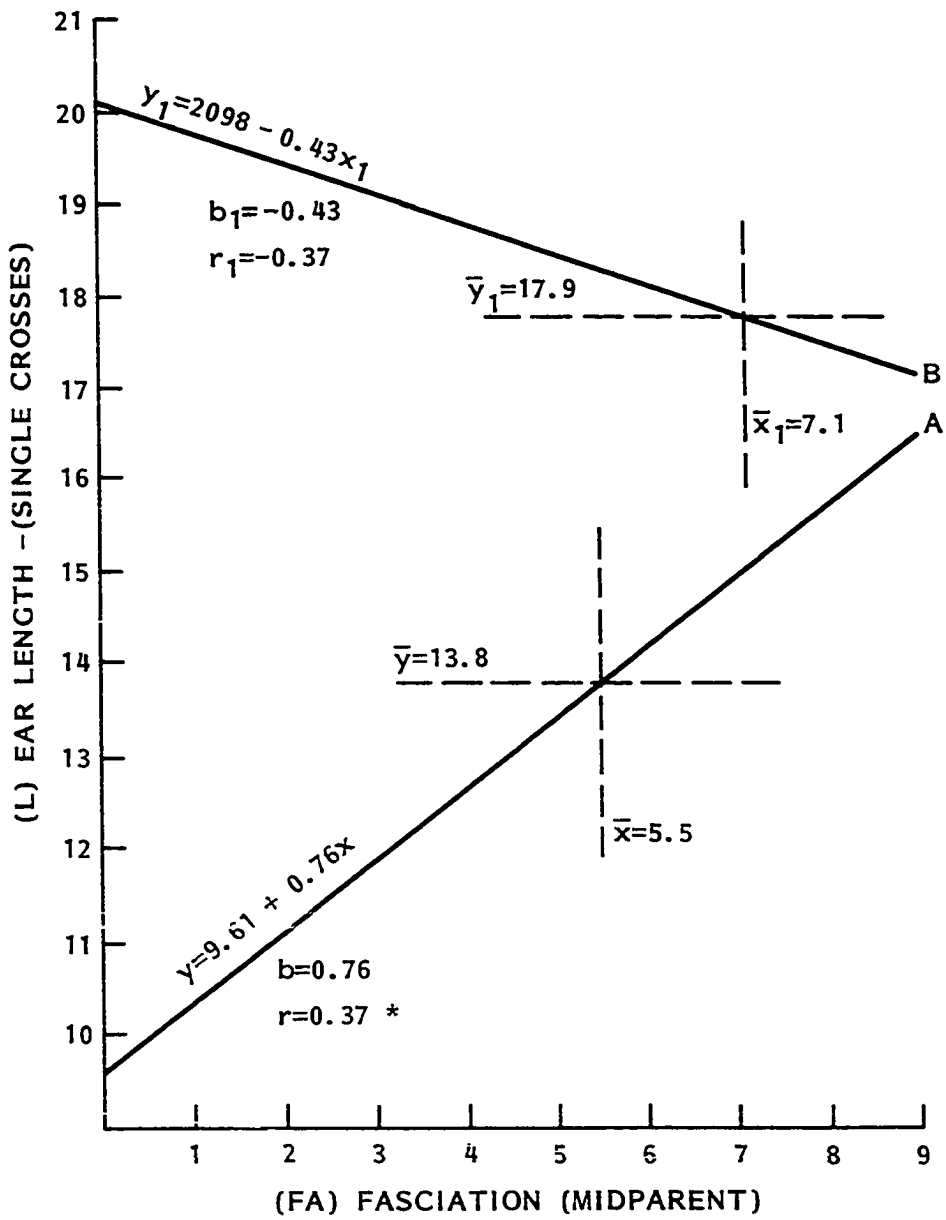

Figure 27. Relationship between fasciation expression (midparent values) and ear length in the single crosses of the diallel trial; A - diallel crosses; B - A632 testcrosses

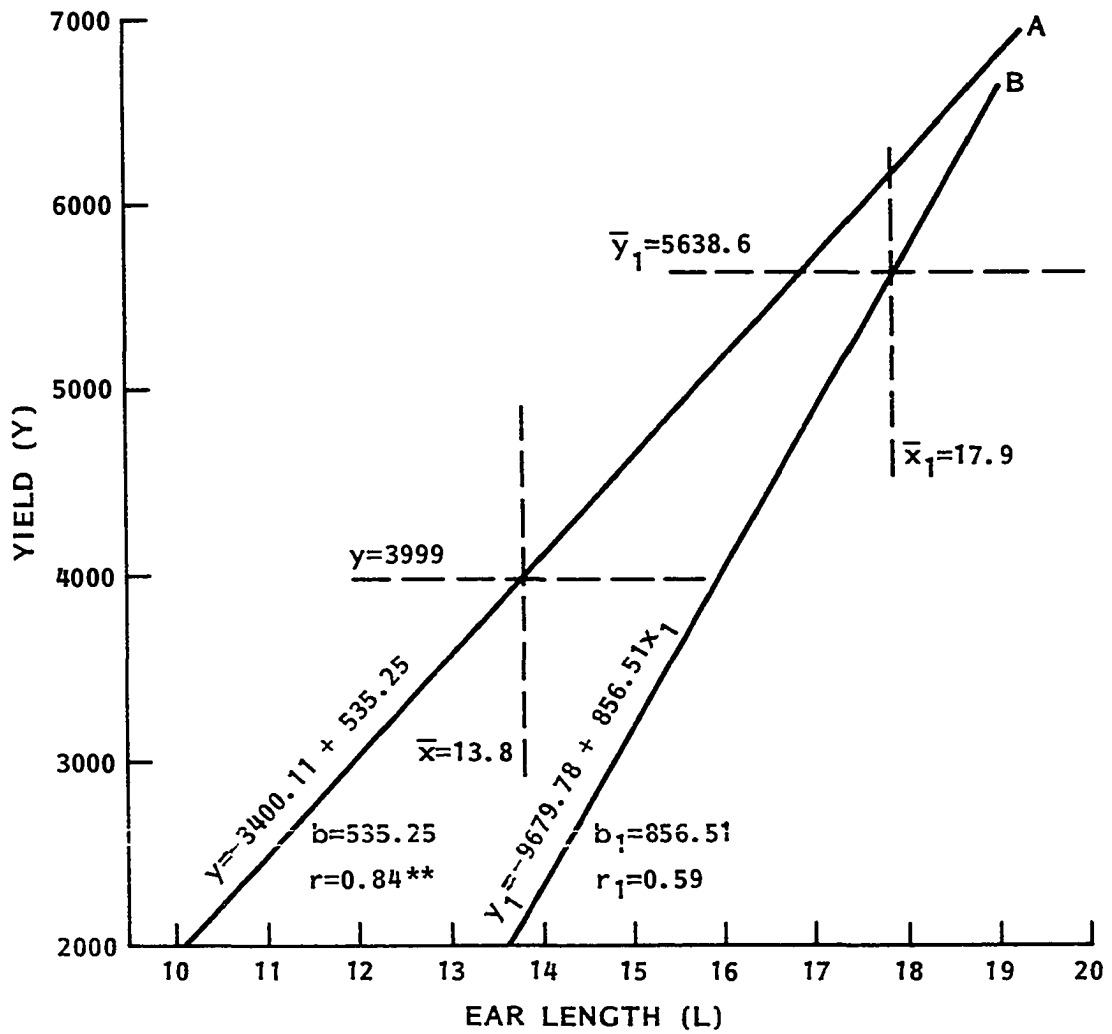

Figure 28. Relationship between yield and ear length for A - diallel crosses and B - A632 testcrosses

diallel crosses and A632 testcrosses (Figure 25) support previous conclusions about the recessiveness of fasciation expression; (b) A632 would be dominant for fasciation and would negate the negative influence of fasciation upon ear length in all testcrosses (Figure 27); (c) as a result of complementary genes for ear length, the testcrosses would take advantage of the strong correlation between fasciation and kernel-row number, improving the yield. This is also suggested when we compare the entry 43 in Table 27 (the best yielding single cross) with A632 x A619 (entry 50 in Table 27), where the major mean differences are for kernel-row number.

The S_1 and S_2 progenies and diallel analyses suggest the following conclusions:

1. Ear length was shown to be consistently the most important trait related with yield.
2. Fasciation expression, however positively correlated with yield in the S_1 progenies (Table 19), may be considered as having some importance in the yield expression. This conclusion is based on: (a) data from Table 20 where FA was responsible for 4.7% in the sum of squares for yield, as the fourth most important trait in a regression model for yield; (b) data from Table 23 show that ear diameter D_5 (the best indicator of the degree of fascia-

tion expression) should be included in a regression model as the fifth parameter, responsible for an increase of 4.1% in the total sum of squares due to yield; and (c) data from yield results of the diallel (Table 27) also support this conclusion.

V. SUMMARY AND CONCLUSIONS

In a collecting program of maize germplasm in Portugal during 1976, a few open-pollinated varieties were found that had a high frequency of a strong fasciation expression of the ears. These varieties had been maintained for a long period of time in some areas surrounded by other open-pollinated varieties. In some of these open-pollinated varieties, the fasciation expression was present in more than 90% of the ears. A breeding program that included the use of this type of germplasm had been developed at a Portuguese maize breeding station (Braga) to increase kernel-row number. As a result of that program, two inbreds had been developed (WF9-R and 38-11/2) and included in the pedigree of a double-cross hybrid (HB19) used in northern Portugal. My study was conducted to gain a better understanding of the inheritance of fasciation expression for six Portuguese Regional Varieties (PRVs) that had different levels of fasciation expression.

Due to the high percentage of fasciation expression and the high level of tassel branching, a study was designed to test both the dominance of the character and possible allelism with the ramosa genes ra1, ra2, and ra3. Crosses were produced between the six selected PRVs and the ramosa sources ra1, ra2, and ra3. From the set of six PRVs, PRV 30 had the most extreme form of fasciation expression.

PRV 30 was studied in detail, including the evaluation of 12 traits: fasciation expression (FA), six ear diameters (D_1 to D_6), two kernel-row counts (R_1 and R_2), ear length (L), stand (STD), and yield (Y).

Two approaches were used in the study of PRV 30. (1) The qualitative genetics approach included a previous study of tassel branching, and an attempt was made to propose some genetic models that would fit the observed values. (2) The quantitative genetics approach included S_1 and S_2 progeny trials for the PRV 30, and a diallel trial that included eight parents (6 PRVs and 2 inbreds), the 28 diallel crosses, and a set of seven testcrosses with the inbred A632. Measurements were made for 12 traits in all trials. Data collected from S_1, S_2, and diallel trials included: analyses of variance and correlation studies; the study of the distributions for the different traits; a multiple regression analysis; and heritabilities estimates were determined for the S_1 and S_2 progenies of PRV 30. Low coefficients of variation (CV) were obtained for all trials (Tables 18, 21, and 24), indicating a good degree of confidence for the data analyzed. My primary objective of these studies was to determine the possible relationships between fasciation expression and yield.

From both the qualitative and quantitative genetics approaches in this study, the following conclusions are

suggested:

1. For the PRVs studied, results indicated that there was no allelism between genes for fasciation expression and the ramosa 1 gene (ral).
2. Fasciation expression in PRV 30 behaved essentially as a recessive character. Some instances of partial dominance were found, but no complete dominance was detected.
3. There was evidence that both ramosa 1 genes (ral) and genes for fasciation were associated with suppressor genes. Such an association would explain why a character, recessive in nature, can have a dominant expression under certain circumstances; this suggested an evolutionary surviving mechanism that permitted expression of the recessive allele. This interesting genetic mechanism would also explain why PRV 30 and other strongly fasciated open-pollinated varieties could maintain a high level of fasciation expression when surrounded by nonfasciated open-pollinated varieties, as it occurs in certain areas of Portugal.
4. Fasciation expression seemed to be a complex trait, influenced by the environment and inherited in a quantitative manner.
5. Heritabilities estimates on a progeny mean basis

for the S_1 progenies, and on a plot mean basis for the S_2 progenies, were very high for all 12 variables except for yield.

6. Results from correlation and multiple regression analyses indicated that the number of parameters evaluated could be substantially reduced: (a) for the study of S_1 progenies, ear length (L), stand (STD), and ear diameter D_2 should be included; (b) for the S_2 progenies, ear length (L), stand (STD), kernel-row number R_1, and ear diameter D_5 would be sufficient; and (3) for the diallel crosses, ear length (L), stand (STD), and ear diameter D_6 were of primary importance.
7. Ear length was, in all cases, highly correlated with yield.
8. Fasciation expression (FA) was always highly correlated with kernel-row number R_1 and R_2, indicating an increase in kernel-row number with increased expression of fasciation.
9. Results from the diallel crosses and A632 testcrosses suggested: (a) additive gene action was preponderant because GCA effects were substantially greater than SCA effects; (b) there was genetic potential for increased yield in the fasciated Portuguese germplasm. This potential would be

conditioned by a mechanism involving the interaction between fasciation (FA) and ear length (L) in the following manner. The negative influence of fasciation expression on yield was not due to a direct action on yield per se, but due to a strong negative effect on the yield component ear length. When crossed with a dominant source (A632), the fasciation expression was reduced, which also reduced the negative influence of fasciation expression on ear length. Under these circumstances, fasciation expression was capable of expressing its genetic potential for yield, probably due to its high correlation with kernel-row number increase. Such a polyvalent relationship among the four parameters (fasciation expression, kernel-row number, ear length, and yield) would provide an answer to the controversial points of view of several authors reported in the literature, about the fasciation character.

10. Fasciation would be a useful trait for improving yield only when under a controlled situation, in ranges of intermediate expressions, with a phenotype of the type ("ff") or (f-), as shown in our qualitative genetics study. This was also the case for the two inbreds, WF9-R and 38-11/2, used as parents in

Portuguese double-cross hybrid, HB19.

11. Due to its genetic complexity and special circumstances under which it could be useful for yield increase, fasciation expression should only be included in long-term breeding programs.
12. Testcrosses of fasciated Portuguese germplasm with the inbred A632 showed the practical advantage of the introduction of exotic germplasm for increasing yield. This practical advantage would be valid for both U.S. and Portuguese breeding programs. These results support the hypothesis of heterotic vigor between dent and flint types.
13. My studies of PRV 30 did not permit me to include it in any of the ten race classifications of Costa-Rodrigues (1969) for the Portuguese maize germplasm. This suggests that--as recommended by Costa-Rodrigues (1969)--further studies in the classification of Portuguese maize germplasm should be undertaken.

VI. LITERATURE CITED

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VII. ACKNOWLEDGMENTS

> The Lord is my strength and my song; He has become my salvation. He is my God, and I will praise Him, my Father's God, and I will exalt Him.
> (Exodus 15:2)

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Plate 32. "Those killed by the sword are better off than those who die of famine; racked with hunger, they waste away for lack of food from the field."

(Lamentations 4:9)

VIII. APPENDIX

Table A1. F_1s from the crosses between PRVs with ramosa sources ra1, ra2, and ra3

Pedigree	Slide #
ra1/ra1 x PRV 30-25	M-1462
ra1/ra1 x PRV 216-21	M-1463
ra1/ra1 x PRV 38-38	M-1464
ra1/ra1 x 38-11/2-34	M-
ra1/ra1 x PRV 99-27	M-1466
+/ra1 x PRV 38-22	M-1467
+/ra1 x PRV 38-48	M-1468
+/ra1 x PRV 30-24	M-1465
+/ra1 x PRV 38-57	M-1470
+/ra1 x 38-11/2-6	M-1471
+/ra1 x PRV 30-15	M-1472
+/ra1 x PRV 99-8	M-1473
+/ra1 x PRV 37-8	M-1474
+/ra1 x PRV 37-16	M-1475
+/ra1 x PRV 99-30	M-1476
+/ra1 x PRV 37-13	M-1477
+/ra1 x PRV 30-3	M-1478
+/ra1 x PRV 37-2	M-1479
+/ra1 x PRV 30-17	M-1480
+/ra1 x PRV 99-119	M-1481
+/ra1 x PRV 38-62	M-1482
+/ra1 x PRV 30-1	M-1483
+/ra1 x PRV 37-18	M-1484
+/ra1 x PRV 99-1	M-1485
+/ra1 x PRV 37-2	M-1486
+/ra1 x PRV 37-9	M-1487
+/ra1 x PRV 37-3	M-1488
+/ra1 x PRV 37-3	M-1489
+/ra1 x PRV 37-3	M-1490
+/ra2-66 x 38-11/2-4	M-1491
+/ra2-66 x 38-11/2-19	M-1492
+/ra2-66 x 38-11/2-2	M-1493
+/ra2-66 x 38-11/2-28	M-1494
+/ra2-66 x 38-11/2-16	M-1495
+/ra2-66 x 38-11/2-32	M-1496
+/ra2-66 x PRV 38-8	M-1497
+/ra2-66 x PRV 38-59	M-1498
+/ra2-66 x PRV 38-9	M-1499
+/ra2-66 x PRV 38-44	M-1500
+/ra2-66 x PRV 38-51	M-1501
+/ra2-66 x PRV 38-60	M-1502
+/ra2-66 x PRV 99-102	M-1503

Table A1. (Continued)

Pedigree	Slide #
+/ra2-66 x PRV 99-76	M-1504
+/ra2-66 x PRV 99-110	M-1505
+/ra2-66 x PRV 99-51	M-1506
+/ra2-66 x PRV 37-40	M-1507
+/ra2-66 x PRV 214-23	M-1508
+/ra2-66 x PRV 30-19	M-1509
+/ra2-66 x PRV 30-35	M-1510
+/ra2-66 x PRV 30-36	M-1511
+/ra2-66 x PRV 30-34	M-1512
+/ra2-66 x PRV 30-22	M-1513
+/ra2-77 x PRV 38-12	M-1514
+/ra2-77 x 38-11/2-29	M-1515
+/ra2-77 x 38-11/2-31	M-1516
+/ra2-77 x 38-11/2-33	M-1517
+/ra2-77 x 38-11/2-26	M-1518
+/ra2-77 x PRV 38-55	M-1519
+/ra2-77 x PRV 38-31	M-1520
+/ra2-77 x PRV 99-105	M-1521
+/ra2-77 x PRV 99-52	M-1522
+/ra2-77 x PRV 99-29	M-1523
+/ra2-77 x PRV 30-47	M-1524
+/ra2-77 x PRV 30-12	M-1525
+/ra2-77 x PRV 216-200	M-1526
+/ra2-77 x PRV 216-201	M-1527
+/ra2-77 x 38-11/2-22	M-1528
+/ra3-68 x PRV 214-24	M-1529
+/ra3-68 x PRV 30-29	M-1530
+/ra3-68 x PRV 30-56	M-1531
+/ra3-68 x PRV 38-52	M-1532
+/ra3-68 x PRV 30-23	M-1533
+/ra3-68 x PRV 37-9	M-1534
+/ra3-68 x PRV 30-44	M-1535
+/ra3-68 x PRV 30-9	M-1536
+/ra3-68 x PRV 37-10	M-1537
+/ra3-68 x PRV 30-5	M-1538
+/ra3-68 x PRV 38-61	M-1539
+/ra3-68 x PRV 99-15	M-1540
+/ra3-68 x PRV 99-33	M-1541
+/ra3-68 x PRV 38-73	M-1542
+/ra3-68 x PRV 99-25	M-1543
+/ra3-68 x PRV 99-17	M-1544
+/ra3-68 x PRV 99-23	M-1545

Table A1. (Continued)

Pedigree	Slide #
+/ra3-68 x PRV 99-16	M-1546
+/ra3-68 x PRV 214-1	M-1547
+/ra3-68 x PRV 214-18	M-1548
+/ra3-68 x PRV 216-9	M-1549
+/ra3-68 x PRV 30-50	M-1550
+/ra3-68 x PRV 38-2	M-1551
+/ra3-68 x 38-11/2-30	M-1552
+/ra3-68 x 38-11/2-39	M-1553
+/ra3-68 x 38-11/2-18	M-1554
+/ra3-68 x 38-11/2-10	M-1555
+/ra3-68 x PRV 30-4	M-1556
+/ra3-69 x PRV 37-2	M-1557
+/ra3-69 x PRV 30-37	M-1558
+/ra3-69 x PRV 30-26	M-1559
+/ra3-69 x PRV 38-71	M-1560
+/ra3-69 x PRV 99-3	M-1561
+/ra3-69 x PRV 38-33	M-1562
+/ra3-69 x PRV 99-2	M-1563
+/ra3-69 x PRV 30-4	M-1564
+/ra3-69 x PRV 216-7	M-1565
+/ra3-69 x PRV 99-7	M-1566
+/ra3-69 x PRV 30-53	M-1567
+/ra3-69 x PRV 214-7	M-1568
+/ra3-69 x PRV 38-49	M-1569
+/ra3-69 x PRV 30-39	M-1570
+/ra3-69 x PRV 30-45	M-1571
+/ra3-69 x PRV 99-123	M-1572
+/ra3-69 x PRV 37-14	M-1573
+/ra3-69 x PRV 37-3	M-1574
+/ra3-69 x PRV 38-34	M-1575
+/ra3-69 x PRV 216-1	M-1576
+/ra3-69 x PRV 38-39	M-1577
+/ra3-69 x PRV 99-1	M-1578
+/ra3-69 x PRV 30-58	M-1579
+/ra3-69 x PRV 216-24	M-1580
+/ra3-69 x PRV 99-19	M-1581
+/ra3-69 x PRV 30-41	M-1582
+/ra3-69 x 38-11/2-25	M-1583
+/ra3-69 x 38-11/2-20	M-1584
+/ra3-69 x 38-11/2-14	M-1585
+/ra3-69 x 38-11/2-12	M-1586
+/ra3-69 x 38-11/2-41	M-1587
+/ra3-69 x 38-11/2-24	M-1588

Table A2. F_2s from the crosses between PRV 30 and the ramosa sources ra1, ra2, and ra3

Pedigree	Slide #
ra1/ra1 x PRV 30-25 (2)[a]	M-1739
ra1/ra1 x PRV 30-25 (9)	M-1740
ra1/ra1 x PRV 30-25 (9)	M-1741
+/ra1 x PRV 30-24 (1)	M-1742
+/ra1 x PRV 30-24 (3)	M-1743
+/ra1 x PRV 30-24 (4)	M-1744
+/ra1 x PRV 30-24 (5)	M-1745
+/ra1 x PRV 30-24 (6)	M-1746
+/ra1 x PRV 30-24 (7)	M-1747
+/ra1 x PRV 30-24 (9)	M-1748
+/ra1 x PRV 30-24 (9)	M-1749
+/ra1 x PRV 30-15 (2)	M-1750
+/ra1 x PRV 30-15 (3)	M-1751
+/ra1 x PRV 30-15 (9)	M-1752
+/ra1 x PRV 30-15 (9)	M-1753
+/ra1 x PRV 30-3 (8)	M-1754
+/ra1 x PRV 30-3 (9)	M-1755
+/ra1 x PRV 30-3 (9)	M-1756
+/ra1 x PRV 30-17 (9)	M-1757
+/ra1 x PRV 30-17 (9)	M-1758
+/ra1 x PRV 30-1 (8)	M-1759
+/ra1 x PRV 30-1 (9)	M-1760
+/ra1 x PRV 30-1 (9)	M-1761
+/ra2-66 x PRV 30-19 (5)	M-1762
+/ra2-66 x PRV 30-19 (7)	M-1763
+/ra2-66 x PRV 30-19 (9)	M-1764
+/ra2-66 x PRV 30-19 (9)	M-1765
+/ra2-66 x PRV 30-35 (8)	M-1766
+/ra2-66 x PRV 30-35 (9)	M-1767
+/ra2-66 x PRV 30-35 (9)	M-1768
+/ra2-66 x PRV 30-36 (2)	M-1769
+/ra2-66 x PRV 30-36 (5)	M-1770
+/ra2-66 x PRV 30-36 (6)	M-1771
+/ra2-66 x PRV 30-36 (9)	M-1772
+/ra2-66 x PRV 30-36 (9)	M-1773
+/ra2-66 x PRV 30-34 (1)	M-1774
+/ra2-66 x PRV 30-34 (3)	M-1775
+/ra2-66 x PRV 30-34 (3)	M-1776
+/ra2-66 x PRV 30-34 (4)	M-1777

[a]The digit within parentheses indicates the fasciation classification of the F_1 ear which originates the F_2.

Table A2. (Continued)

Pedigree	Slide #
+/ra2-66 x PRV 30-34 (4)	M-1778
+/ra2-66 x PRV 30-34 (5)	M-1779
+/ra2-66 x PRV 30-34 (6)	M-1780
+/ra2-66 x PRV 30-34 (9)	M-1781
+/ra2-66 x PRV 30-34 (9)	M-1782
+/ra2-66 x PRV 30-22 (3)	M-1783
+/ra2-66 x PRV 30-22 (9)	M-1784
+/ra2-66 x PRV 30-22 (9)	M-1785
+/ra2-77 x PRV 30-47 (5)	M-1786
+/ra2-77 x PRV 30-47 (9)	M-1787
+/ra2-77 x PRV 30-47 (9)	M-1788
+/ra2-77 x PRV 30-12 (8)	M-1789
+/ra2-77 x PRV 30-12 (9)	M-1790
+/ra2-77 x PRV 30-12 (9)	M-1791
+/ra2-77 x PRV 30-12 (9)	M-1792
+/ra3-68 x PRV 30-29 (8)	M-1793
+/ra3-68 x PRV 30-29 (9)	M-1794
+/ra3-68 x PRV 30-29 (9)	M-1795
+/ra3-68 x PRV 30-56 (3)	M-1796
+/ra3-68 x PRV 30-56 (4)	M-1797
+/ra3-68 x PRV 30-56 (4)	M-1798
+/ra3-68 x PRV 30-56 (9)	M-1799
+/ra3-68 x PRV 30-56 (9)	M-1800
+/ra3-68 x PRV 30-23 (3)	M-1801
+/ra3-68 x PRV 30-23 (5)	M-1802
+/ra3-68 x PRV 30-23 (9)	M-1803
+/ra3-68 x PRV 30-23 (9)	M-1804
+/ra3-68 x PRV 30-44 (8)	M-1805
+/ra3-68 x PRV 30-44 (9)	M-1806
+/ra3-68 x PRV 30-44 (9)	M-1807
+/ra3-68 x PRV 30-9 (5)	M-1808
+/ra3-68 x PRV 30-9 (9)	M-1809
+/ra3-68 x PRV 30-9 (9)	M-1810
+/ra3-68 x PRV 30-5 (1)	M-1811
+/ra3-68 x PRV 30-5 (2)	M-1812
+/ra3-68 x PRV 30-5 (2)	M-1813
+/ra3-68 x PRV 30-5 (4)	M-1814
+/ra3-68 x PRV 30-5 (5)	M-1815
+/ra3-68 x PRV 30-5 (5)	M-1816
+/ra3-68 x PRV 30-5 (9)	M-1817
+/ra3-68 x PRV 30-5 (9)	M-1818
+/ra3-68 x PRV 30-50 (3)	M-1819
+/ra3-68 x PRV 30-50 (3)	M-1820
+/ra3-68 x PRV 30-50 (3)	M-1821

Table A2. (Continued)

Pedigree	Slide #
+/ra3-68 x PRV 30-50 (9)	M-1822
+/ra3-68 x PRV 30-50 (9)	M-1823
+/ra3-68 x PRV 30-4 (9)	M-1824
+/ra3-68 x PRV 30-4 (9)	M-1825
+/ra3-69 x PRV 30-57 (3)	M-1826
+/ra3-69 x PRV 30-57 (4)	M-1827
+/ra3-69 x PRV 30-57 (4)	M-1828
+/ra3-69 x PRV 30-57 (4)	M-1829
+/ra3-69 x PRV 30-57 (4)	M-1830
+/ra3-69 x PRV 30-57 (4)	M-1831
+/ra3-69 x PRV 30-57 (9)	M-1832
+/ra3-69 x PRV 30-57 (9)	M-1833
+/ra3-69 x PRV 30-26 (4)	M-1834
+/ra3-69 x PRV 30-26 (6)	M-1835
+/ra3-69 x PRV 30-26 (6)	M-1836
+/ra3-69 x PRV 30-26 (6)	M-1837
+/ra3-69 x PRV 30-26 (9)	M-1838
+/ra3-69 x PRV 30-26 (9)	M-1839
+/ra3-69 x PRV 30-4 (3)	M-1840
+/ra3-69 x PRV 30-4 (9)	M-1841
+/ra3-69 x PRV 30-53 (3)	M-1842
+/ra3-69 x PRV 30-53 (4)	M-1843
+/ra3-69 x PRV 30-53 (9)	M-1844
+/ra3-69 x PRV 30-53 (9)	M-1845
+/ra3-69 x PRV 30-39 (8)	M-1846
+/ra3-69 x PRV 30-39 (9)	M-1847
+/ra3-69 x PRV 30-39 (9)	M-1848
+/ra3-69 x PRV 30-45 (9)	M-1849
+/ra3-69 x PRV 30-45 (9)	M-1850
+/ra3-69 x PRV 30-58 (4)	M-1851
+/ra3-69 x PRV 30-58 (5)	M-1852
+/ra3-69 x PRV 30-58 (9)	M-1853
+/ra3-69 x PRV 30-58 (9)	M-1854
+/ra3-69 x PRV 30-41 (3)	M-1855
+/ra3-69 x PRV 30-41 (5)	M-1856
+/ra3-69 x PRV 30-41 (4)	M-1857
+/ra3-69 x PRV 30-41 (4)	M-1858
+/ra3-69 x PRV 30-41 (5)	M-1859
+/ra3-69 x PRV 30-41 (5)	M-1860
+/ra3-69 x PRV 30-41 (9)	M-1861
+/ra3-69 x PRV 30-41 (9)	M-1862

Table A3. S_1s from the selfed males in 1979

Pedigree	Slide #
PRV 30-25	M-1589
PRV 30-24	M-1590
PRV 30-15	M-1591
PRV 30-3	M-1592
PRV 30-17	M-1593
PRV 30-1	M-
PRV 30-57	M-1594
PRV 30-26	M-1595
PRV 30-4	M-1596
PRV 30-53	M-1597
PRV 30-39	M-1598
PRV 30-45	M-1599
PRV 30-58	M-1600
PRV 30-41	M-1601
PRV 30-29	M-1602
PRV 30-56	M-1603
PRV 30-23	M-1604
PRV 30-44	M-1605
PRV 30-9	M-1606
PRV 30-5	M-1607
PRV 30-50	M-1608
PRV 30-47	M-1609
PRV 30-12	M-1610
PRV 30-19	M-1611
PRV 30-35	M-1612
PRV 30-36	M-1613
PRV 30-34	M-1614
PRV 30-22	M-1615
PRV 30-4	M-1616
PRV 37-8	M-1617
PRV 37-16	M-1618
PRV 37-13	M-1619
PRV 37-2	M-1620
PRV 37-18	M-1621
PRV 37-14	M-1622
PRV 37-13	M-1623
PRV 37-43	M-1624
PRV 37-9	M-1625
PRV 37-10	M-1626
PRV 37-6	M-1627
PRV 37-40	M-1628

Table A3. (Continued)

Pedigree	Slide #
PRV 38-38	M-
PRV 38-22	M-1630
PRV 38-48	M-1631
PRV 38-57	M-1632
PRV 38-62	M-1633
PRV 38-71	M-1634
PRV 38-33	M-1635
PRV 38-49	M-1636
PRV 38-41	M-1637
PRV 38-34	M-1638
PRV 38-39	M-1639
PRV 38-52	M-1640
PRV 38-61	M-1641
PRV 38-73	M-1642
PRV 38-2	M-1643
PRV 38-12	M-1644
PRV 38-55	M-1645
PRV 38-31	M-1646
PRV 38-8	M-1647
PRV 38-59	M-1648
PRV 38-9	M-1649
PRV 38-44	M-1650
PRV 38-51	M-1651
PRV 38-60	M-1652
PRV 99-27	M-1653
PRV 99-8	M-
PRV 99-30	M-1654
PRV 99-80	M-1655
PRV 99-119	M-1656
PRV 99-1	M-1657
PRV 99-5	M-1658
PRV 99-3	M-1659
PRV 99-2	M-1660
PRV 99-7	M-1661
PRV 99-123	M-1662
PRV 99-1	M-1663
PRV 99-19	M-1664
PRV 99-18	M-1665
PRV 99-4	M-1666
PRV 99-128	M-1667
PRV 99-15	M-1668
PRV 99-33	M-1669
PRV 99-25	M-1670

Table A3. (Continued)

Pedigree	Slide #
PRV 99-17	M-1671
PRV 99-23	M-1672
PRV 99-24	M-1673
PRV 99-26	M-1674
PRV 99-16	M-1675
PRV 99-105	M-1676
PRV 99-52	M-1677
PRV 99-29	M-1678
PRV 99-102	M-1679
PRV 99-76	M-1680
PRV 99-110	M-1681
PRV 99-51	M-1862
PRV 185-3	M-1683
PRV 185-2	M-1684
PRV 185-1	M-1685
PRV 214-3	M-1686
PRV 214-12	M-1687
PRV 214-9	M-1688
PRV 214-7	M-1689
PRV 214-10	M-1690
PRV 214-24	M-1691
PRV 214-14	M-1692
PRV 214-1	M-1693
PRV 214-18	M-1694
PRV 214-22	M-1695
PRV 214-20	M-1696
PRV 214-23	M-1697
PRV 214-13	M-1698
PRV 216-21	M-1699
PRV 216-3	M-1700
PRV 216-12	M-
PRV 216-13	M-1701
PRV 216-7	M-1702
PRV 216-1	M-1703
PRV 216-2	M-1704
PRV 216-24	M-1705
PRV 216-100	M-1706
PRV 216-9	M-1707
PRV 216-4	M-1708
PRV 216-10	M-1709
PRV 216-200	M-1710
PRV 216-18	M-1711

Table A3. (Continued)

Pedigree	Slide #
PRV 216-201	M-1712
PRV 216-20	M-1713
PRV 216-6	M-1714
PRV 216-17	M-1715
38-11/2-34	M-1716
38-11/2-6	M-1717
38-11/2-25	M-1718
38-11/2-20	M-1719
38-11/2-14	M-1720
38-11/2-12	M-1721
38-11/2-41	M-1722
38-11/2-24	M-1723
38-11/2-30	M-1724
38-11/2-39	M-1725
38-11/2-18	M-1726
38-11/2-10	M-1727
38-11/2-29	M-1728
38-11/2-31	M-1729
38-11/2-33	M-1730
38-11/2-26	M-1731
38-11/2-22	M-1732
38-11/2-4	M-1733
38-11/2-19	M-1734
38-11/2-2	M-1735
38-11/2-28	M-1736
38-11/2-16	M-1737
38-11/2-32	M-1738

Table A4. Means of the F_1 crosses for fasciation intensity, tassel classification, and kernel-row number

Pedigree	Fasciation (F.)	Tassel (T.)	Row number (R.)
ra1ra1 x PRV 30-25	9.0	7	15.3
+ ra1 x PRV 30-24	6.3	6	18.5
+ ra1 x PRV 30-15	6.8	6	17.0
+ ra1 x PRV 30-3	8.9	6	15.3
+ ra1 x PRV 30-17	6.7	7	16.3
+ ra1 x PRV 30-1	6.2	7	18.6
+ ra2 x PRV 30-19	8.1	7	17.9
+ ra2 x PRV 30-35	8.1	7	16.8
+ ra2 x PRV 30-36	5.7	7	20.1
+ ra2 x PRV 30-34	6.9	7	17.9
+ ra2 x PRV 30-22	5.7	6	16.8
+ ra2 x PRV 30-47	7.6	7	15.4
+ ra2 x PRV 30-12	7.8	7	15.2
+ ra3 x PRV 30-29	7.1	6	16.2
+ ra3 x PRV 30-56	4.7	7	19.6
+ ra3 x PRV 30-23	6.6	6	17.2
+ ra3 x PRV 30-44	7.6	6	17.1
+ ra3 x PRV 30-9	6.7	6	17.1
+ ra3 x PRV 30-5	5.5	6	16.5
+ ra3 x PRV 30-50	7.5	8	16.8
+ ra3 x PRV 30-4	8.3	6	17.3
+ ra3 x PRV 30-57	5.2	6	16.9
+ ra3 x PRV 30-26	7.5	5	16.9
+ ra3 x PRV 30-4	6.7	6	16.4
+ ra3 x PRV 30-53	5.4	5	17.3
+ ra3 x PRV 30-39	7.4	6	15.5
+ ra3 x PRV 30-45	7.0	6	17.8
+ ra3 x PRV 30-58	7.3	6	17.0
	F.. = 6.9	T.. = 6.4	R.. = 17.1

Table A5. Means of the F_2 generations for fasciation intensity, tassel classification, and kernel-row number

Pedigree	Fasciation (F.)	Tassel (T.)	Row number (R.)
ral/ral x PRV 30-25	5.0	5.8	16.3
	7.4	4.4	18.0
	8.0	6.3	15.8
+ ral x PRV 30-24	5.3	5.7	15.5
	6.7	7.0	17.3
	3.7	6.7	18.5
	4.4	6.8	17.5
	6.0	6.3	18.0
	4.0	6.3	16.8
	6.0	6.8	14.0
	5.9	6.9	15.8
+ ral x PRV 30-15	6.5	5.5	15.4
	4.7	6.8	17.0
	7.5	6.5	15.3
	8.2	5.3	15.5
+ ral x PRV 30-3	6.0	5.6	16.0
	5.2	7.6	16.5
	7.8	5.4	15.0
+ ral x PRV 30-17	8.3	7.3	14.3
	7.5	7.0	15.0
+ ral x PRV 30-1	4.6	6.6	17.9
	7.1	6.6	17.3
	7.4	6.8	13.3
+ ra2 x PRV 30-19	5.0	7.0	17.0
	5.3	6.3	15.0
	4.0	7.0	19.3
	7.9	6.5	15.7
+ ra2 x PRV 30-35	5.9	7.4	18.1
	7.8	6.8	15.4
	5.3	7.2	17.2
+ ra2 x PRV 30-36	3.6	7.4	18.4
	4.5	8.0	17.5
	4.7	7.3	18.4
	6.7	7.0	16.1
	5.5	7.0	16.5

Table A5. (Continued)

Pedigree	Fasciation (F.)	Tassel (T.)	Row number (R.)
+ *ra2* x PRV 30-34	4.8	7.4	19.8
	3.9	7.1	20.2
	3.8	7.8	18.7
	5.0	7.7	17.8
	6.0	7.2	19.1
	5.1	6.8	16.8
	5.3	7.3	21.8
	6.6	7.1	17.8
	6.3	6.8	15.0
+ *ra2* x PRV 30-22	4.0	5.3	18.9
	8.3	5.6	17.2
	6.7	6.6	14.0
+ *ra2* x PRV 30-47	6.2	7.1	14.1
	6.9	7.2	14.8
	5.2	7.0	15.0
+ *ra2* x PRV 30-12	5.0	6.3	19.0
	5.6	6.5	16.1
	6.4	6.9	14.8
	7.3	6.4	16.7
+ *ra3* x PRV 30-29	6.2	6.8	16.8
	5.6	7.2	15.3
	9.0	6.0	12.8
+ *ra3* x PRV 30-56	3.8	7.2	19.4
	5.2	7.3	18.8
	4.4	7.5	19.9
	6.0	7.1	17.0
	6.5	6.8	16.7
+ *ra3* x PRV 30-23	3.7	4.8	22.2
	6.4	5.6	16.6
	7.3	6.3	15.0
	7.5	5.4	14.8
+ *ra3* x PRV 30-44	7.7	6.4	19.8
	8.7	5.3	15.2
	8.5	6.0	13.1
+ *ra3* x PRV 30-9	6.4	6.0	18.7
	8.5	5.4	14.6
	7.7	5.3	14.7

Table A5. (Continued)

Pedigree	Fasciation (F.)	Tassel (T.)	Row number (R.)
+ ra3 x PRV 30-5	5.4	7.3	16.8
	5.9	5.9	18.7
	6.7	5.8	16.2
	5.5	6.3	17.1
	4.7	6.4	19.4
	4.9	6.6	15.9
	7.9	6.5	15.8
	5.8	7.5	17.4
+ ra3 x PRV 30-50	5.1	7.2	17.4
	3.7	6.8	19.0
	6.3	6.8	16.0
	8.7	6.2	13.4
	8.2	6.6	13.3
+ ra3 x PRV 30-4	7.6	5.9	15.3
	7.7	6.0	16.0
+ ra3 x PRV 30-57	3.5	5.5	19.5
	5.8	3.8	17.3
	4.0	6.0	24.0
	4.8	3.4	17.0
	4.7	5.0	17.5
	5.0	5.0	15.0
	6.7	4.7	15.0
	6.7	4.6	15.6
+ ra3 x PRV 30-26	4.7	4.4	15.5
	5.5	4.5	17.1
	6.1	5.1	18.7
	4.6	4.3	20.4
	7.8	5.7	16.3
	6.3	4.9	17.7
+ ra3 x PRV 30-4	6.2	4.7	16.3
	7.1	6.0	15.0
+ ra3 x PRV 30-53	5.6	4.8	16.3
	5.3	5.0	16.0
	8.3	5.2	18.0
	9.0	5.8	16.0

Table A5. (Continued)

Pedigree	Fasciation (F.)	Tassel (T.)	Row number (R.)
+ ra3 x PRV 30-39	5.6	5.2	17.6
	9.0	5.8	13.0
	8.8	5.3	14.3
+ ra3 x PRV 30-45	6.1	5.0	16.0
	5.5	7.5	15.0
+ ra3 x PRV 30-58	6.1	6.6	16.4
	6.8	6.3	17.3
	8.9	5.7	15.0
	7.7	6.0	16.7
+ ra3 x PRV 30-41	5.0	3.4	19.3
	6.8	3.6	15.0
	5.4	4.0	17.3
	8.1	4.0	15.9
	7.5	3.3	15.0
	6.6	4.8	18.6
	8.5	4.9	14.1
	8.5	5.3	15.6
	F.. = 6.2	T.. = 6.1	R.. = 16.5

Table A6. Means of the S_1 progenies for fasciation intensity, tassel classification, and kernel-row number

Pedigree	Fasciation (F.)	Tassel (T.)	Row number (R.)
PRV 30-24	3.0	5.0	-
PRV 30-15	4.3	5.0	24.3
PRV 30-3	4.4	4.6	14.7
PRV 30-17	5.9	5.0	17.1
PRV 30-57	3.7	4.0	21.7
PRV 30-26	3.3	5.3	19.0
PRV 30-4	3.8	5.3	18.0
PRV 30-53	4.0	5.0	17.0
PRV 30-39	4.0	4.5	15.5
PRV 30-45	7.3	5.0	13.7
PRV 30-58	4.4	5.4	12.5
PRV 30-41	4.0	5.0	27.0
PRV 30-29	3.4	5.0	22.8
PRV 30-56	2.0	7.6	29.3
PRV 30-23	3.3	4.7	21.0
PRV 30-44	5.0	5.0	14.0
PRV 30-9	5.3	4.2	16.4
PRV 30-5	3.2	6.5	25.3
PRV 30-50	3.7	6.3	18.6
PRV 30-47	3.7	6.4	17.6
PRV 30-12	4.2	5.0	20.2
PRV 30-19	4.0	5.7	15.6
PRV 30-35	4.2	6.3	18.7
PRV 30-36	4.0	6.0	18.0
PRV 30-34	2.8	5.7	22.8
PRV 30-22	5.1	5.6	16.8
PRV 30-4	3.3	5.8	15.0
	F.. = 4.0	T.. = 5.2	R.. = 19.0

Table A7. Listing of pedigrees of the S_1s

Entry no.	Pedigree name
1	ra1ra1 x PRV 30-25-9
2	ra1ra1 x PRV 30-25-9
3	ra1ra1 x PRV 30-25-9
4	+ ra1 x PRV 30-24-1
5	+ ra1 x PRV 30-24-3
6	+ ra1 x PRV 30-24-4
7	+ ra1 x PRV 30-24-5
8	+ ra1 x PRV 30-24-9
9	+ ra1 x PRV 30-15-2
10	+ ra1 x PRV 30-15-3
11	+ ra1 x PRV 30-15-9
12	+ ra1 x PRV 30-15-9
13	+ ra1 x PRV 30-3-8
14	+ ra1 x PRV 30-3-9
15	+ ra1 x PRV 30-3-9
16	+ ra1 x PRV 30-17-9
17	+ ra1 x PRV 30-17-9
18	+ ra1 x PRV 30-1-8
19	+ ra1 x PRV 30-1-9
20	+ ra1 x PRV 30-1-9
21	+ ra2-66 x PRV 30-19-7
22	+ ra2-66 x PRV 30-19-9
23	+ ra2-66 x PRV 30-19-9
24	+ ra2-66 x PRV 30-35-8
25	+ ra2-66 x PRV 30-35-9
26	+ ra2-66 x PRV 30-35-9
27	+ ra2-66 x PRV 30-36-2
28	+ ra2-66 x PRV 30-36-5
29	+ ra2-66 x PRV 30-36-6
30	+ ra2-66 x PRV 30-36-9
31	+ ra2-66 x PRV 30-34-1
32	+ ra2-66 x PRV 30-34-3
33	+ ra2-66 x PRV 30-34-4
34	+ ra2-66 x PRV 30-34-5
35	+ ra2-66 x PRV 30-34-9
36	+ ra2-66 x PRV 30-22-3
37	+ ra2-66 x PRV 30-22-9
38	+ ra2-66 x PRV 30-22-9
39	+ ra2-77 x PRV 30-47-5
40	+ ra2-77 x PRV 30-47-9
41	+ ra2-77 x PRV 30-47-9
42	+ ra2-77 x PRV 30-12-8
43	+ ra2-77 x PRV 30-12-9
44	+ ra2-77 x PRV 30-12-9

Table A7. (Continued)

Entry no.	Pedigree name
45	+ ra2-77 x PRV 30-12-9
46	+ ra3-68 x PRV 30-29-8
47	+ ra3-68 x PRV 30-29-9
48	+ ra3-68 x PRV 30-29-9
49	+ ra3-68 x PRV 30-56-3
50	+ ra3-68 x PRV 30-56-4
51	+ ra3-68 x PRV 30-56-4
52	+ ra3-68 x PRV 30-56-9
53	+ ra3-68 x PRV 30-23-3
54	+ ra3-68 x PRV 30-23-5
55	+ ra3-68 x PRV 30-23-9
56	+ ra3-68 x PRV 30-23-9
57	+ ra3-68 x PRV 30-44-8
58	+ ra3-68 x PRV 30-44-9
59	+ ra3-68 x PRV 30-44-9
60	+ ra3-68 x PRV 30-9-5
61	+ ra3-68 x PRV 30-9-9
62	+ ra3-68 x PRV 30-9-9
63	+ ra3-68 x PRV 30-5-1
64	+ ra3-68 x PRV 30-5-2
65	+ ra3-68 x PRV 30-5-4
66	+ ra3-68 x PRV 30-5-5
67	+ ra3-68 x PRV 30-5-9
68	+ ra3-68 x PRV 30-50-3
69	+ ra3-68 x PRV 30-50-3
70	+ ra3-68 x PRV 30-50-3
71	+ ra3-68 x PRV 30-50-9
72	+ ra3-68 x PRV 30-4-9
73	+ ra3-68 x PRV 30-4-9
74	+ ra3-69 x PRV 30-57-3
75	+ ra3-69 x PRV 30-57-4
76	+ ra3-69 x PRV 30-57-4
77	+ ra3-69 x PRV 30-57-9
78	+ ra3-69 x PRV 30-26-4
79	+ ra3-69 x PRV 30-26-6
80	+ ra3-69 x PRV 30-26-6
81	+ ra3-69 x PRV 30-26-9
82	+ ra3-69 x PRV 30-4-3
83	+ ra3-69 x PRV 30-4-9
84	+ ra3-69 x PRV 30-53-3
85	+ ra3-69 x PRV 30-53-4
86	+ ra3-69 x PRV 30-53-9
87	+ ra3-69 x PRV 30-53-9
88	+ ra3-69 x PRV 30-39-8

Table A7. (Continued)

Entry no.	Pedigree name
89	+ ra3-69 x PRV 30-39-9
90	+ ra3-69 x PRV 30-39-9
91	+ ra3-69 x PRV 30-45-9
92	+ ra3-69 x PRV 30-45-9
93	+ ra3-69 x PRV 30-58-4
94	+ ra3-69 x PRV 30-58-5
95	+ ra3-69 x PRV 30-58-9
96	+ ra3-69 x PRV 30-58-9
97	+ ra3-69 x PRV 30-41-3
98	+ ra3-69 x PRV 30-41-4
99	+ ra3-69 x PRV 30-41-5
100	+ ra3-69 x PRV 30-41-9

Table A8. Listing of pedigrees of the S_2s

Entry no.	Pedigree name
1	PRV 30-15-1
2	PRV 30-15-2
3	PRV 30-15-3
4	PRV 30-15-5
5	PRV 30-15-6
6	PRV 30-15-10
7	PRV 30-3-2
8	PRV 30-3-3
9	PRV 30-3-4
10	PRV 30-17-1
11	PRV 30-17-2
12	PRV 30-17-4
13	PRV 30-17-5
14	PRV 30-17-6
15	PRV 30-17-8
16	PRV 30-17-9
17	PRV 30-57-1
18	PRV 30-57-3

Table A8. (Continued)

Entry no.	Pedigree name
19	PRV 30-26-1
20	PRV 30-26-2
21	PRV 30-26-3
22	PRV 30-26-4
23	PRV 30-26-5
24	PRV 30-26-6
25	PRV 30-4-3
26	PRV 30-4-4
27	PRV 30-4-5
28	PRV 30-53-1
29	PRV 30-53-2
30	PRV 30-39-1
31	PRV 30-39-2
32	PRV 30-45-1
33	PRV 30-45-2
34	PRV 30-45-4
35	PRV 30-58-3
36	PRV 30-41-1
37	PRV 30-29-1
38	PRV 30-29-2
39	PRV 30-29-3
40	PRV 30-56-2
41	PRV 30-56-3
42	PRV 30-23-1
43	PRV 30-23-3
44	PRV 30-44-1
45	PRV 30-9-1
46	PRV 30-9-2
47	PRV 30-9-3
48	PRV 30-9-4
49	PRV 30-9-5
50	PRV 30-9-6
51	PRV 30-5-1
52	PRV 30-5-2
53	PRV 30-5-3
54	PRV 30-50-1
55	PRV 30-50-2
56	PRV 30-50-3
57	PRV 30-50-4
58	PRV 30-50-6
59	PRV 30-47-1
60	PRV 30-47-2
61	PRV 30-47-3
62	PRV 30-12-1

Table A8. (Continued)

Entry no.	Pedigree name
63	PRV 30-12-2
64	PRV 30-12-3
65	PRV 30-12-4
66	PRV 30-12-5
67	PRV 30-12-6
68	PRV 30-12-7
69	PRV 30-12-8
70	PRV 30-12-9
71	PRV 30-12-10
72	PRV 30-19-1
73	PRV 30-19-2
74	PRV 30-19-3
75	PRV 30-19-4
76	PRV 30-35-1
77	PRV 30-35-2
78	PRV 30-35-3
79	PRV 30-36-1
80	PRV 30-34-1
81	PRV 30-34-2
82	PRV 30-34-3
83	PRV 30-34-4
84	PRV 30-34-5
85	PRV 30-22-1
86	PRV 30-22-3
87	PRV 30-22-4
88	PRV 30-22-5
89	PRV 30-4-2
90	PRV 30-4-3
91	+ ra1
92	+ ra2
93	+ ra3
94	WF9-R
95	PRV 38-57
96	PRV 99-7
97	H99
98	B87
99	A619
100	A632